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A PLASMA PROTEIN MARKER FOR POPULATION GENETIC STUDIES OF THE DESERT TORTOISE (*XEROBATES AGASSIZI*)

James L. Glenn[1,2], Richard C. Straight[1], and Jack W. Sites, Jr.[3]

ABSTRACT.—Fifty-seven individual plasma samples from desert tortoises (*Xerobates agassizi*) representing 10 separate populations were analyzed by polyacrylamide gel electrophoresis using alkaline buffers. An albumin-like protein was found to be polymorphic for two electromorphs in northern populations inhabiting the Mohave Desert Province, while Sonoran Desert populations to the south were monomorphic. The genetic divergence demonstrated in this survey is similar to earlier studies and provides evidence for the Colorado River as a potential barrier to gene flow among tortoise populations. These data suggest that tortoise plasma, examined by various electrophoretic methods, may provide a nondestructive means of determining the broad regional origin of desert tortoises.

Desert tortoises (*Xerobates agassizi*) presently inhabit two regions of southwestern Utah, separated east and west by the Beaver Dam Mountains. The population dynamics of the Beaver Dam Slope tortoises (west of the mountains) have been severely impacted by both human and animal activities during the past several decades. Despite both federal and state protective regulations, tortoise numbers in the slope region are probably at an all-time low (Mike Coffeen, UDWR, personal communication). Two stable populations near St. George, east of the Beaver Dam Mountains, face new human development projects that threaten the future of these previously isolated populations. The eastern populations are found in Paradise and City Creek canyons, and relocation of some tortoises from these populations is presently under consideration by the Utah Division of Wildlife Resources. However, several relocation issues remain unresolved, including methods of collection, conditioning, transport, sex ratios, and specimen numbers involved. One problem to be addressed is the question of genetic compatibility of Utah's tortoise populations, especially if any of the tortoises east of the Beaver Dam Mountains are translocated to the western slope.

Few data are available comparing the physiology or morphology of Utah's separate tortoise populations. Rainboth et al. (1989) electrophoretically analyzed whole blood homogenates of 146 desert tortoises from two separate localities in California for allozyme expression at 23 loci. The two populations were quite similar, as each locality contained unique elements only when allozyme combinations were used and there was a considerable degree of overlap in allozyme frequency. Lamb et al. (1989) included five tortoises from Paradise Canyon in an analysis of phylogeographic patterns in mitochondrial DNA (mtDNA) of the gopher tortoise complex. Their data indicated that these individuals fit within an eastern Mohave "clone" representing the northern Arizona and eastern Nevada region. Also, Jennings (1985) included five tortoises from the Beaver Dam Slope region

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TABLE 1. Genotypes and variability estimates for the polymorphic GP-1 locus resolved in 10 localities of *Xerobates agassizi*.

Locality	N	Number of GP-1 genotypes	A*	H**
1. Pima Co., AZ	3	3AA	1.0	0.0
2. Tucson, AZ	6	6AA	1.0	0.0
3. Pinal Co., AZ	4	4AA	1.0	0.0
4. Maricopa Co., AZ	4	4AA	1.0	0.0
5. Kingman, AZ	3	2AA:1BB	1.3	0.0
6. Beaver Dam Slope, AZ	12	9AA:2AB:1BB	1.5	0.083
7. Paradise Canyon, UT	12	3AA:6AB:3BB	1.5	0.208
8. Lincoln Co., NV	2	1AA:1AB	1.5	0.250
9. Riverside Co., CA	4	1AA:3AB	1.5	0.375
10. San Bernardino Co., CA	7	3AA:4AB	1.5	0.214

* = mean number of alleles/locus.
** = mean heterozygosity-direct count.

in biogeographic investigations comparing blood and tissue enzymes using horizontal starch gel electrophoresis. His study included no specimens from east of the Beaver Dam Mountains in Utah but showed that a north-to-south variation was evident and that the Arizona Beaver Dam Slope specimens fit within the northern (Mohavean) group.

Mitochondrial DNA and isozyme studies are costly and may involve traumatic (to the tortoise) and labor-intensive biopsies of internal tissue or the sacrificing of specimens for necropsy. The purpose of this study was to determine whether general proteins in tortoise plasma could be used to detect geographical differences in tortoise populations. Our primary interest was to compare plasma proteins among Utah's aforementioned tortoise populations using alkaline polyacrylamide gel electrophoresis. However, as electrophoretic profiles of plasma or serum from *Xerobates agassizi* have not been previously reported, we examined plasma profiles from tortoises from Arizona, California, and Nevada as well. This report follows the taxonomic grouping of gopher tortoises by Bramble (1982) and the nomenclature revision of Bour and Dubois (1984), applying *Xerobates* as the genus for the desert tortoise.

MATERIALS AND METHODS

Study Area and Sampling

A total of 68 desert tortoises were collected from 11 localities in Arizona (AZ), California (CA), Nevada (NV), and Utah (UT), representing most of the range of this species in the United States. Plasma samples were collected in heparinized tubes (3 ml) by venapuncture (jugular vein or antebrachial sinus) from 15 tortoises from the Beaver Dam Slope, AZ, and Paradise Canyon, UT. Additional plasma samples were donated by colleagues involved in desert tortoise projects in other parts of AZ, and in CA and NV. Localities and sample sizes for the populations sampled are listed in Table 1, and their geographic locations are plotted in Fig. 1.

Electrophoresis

Plasma samples were lyophilized and stored at 4 C. Polyacrylamide gel electrophoresis (PAGE) was run in a Bio-Rad vertical-slab electrophoresis cell, Model 220. The gel was 1.5 mm thick. Sample wells 10 mm long were formed with Canalco stacking gel (2.5% acrylamide). The 7% acrylamide separating gel was 80 mm in length. Samples were electrophoresed toward the anode (+) at 20 mA constant current and were stopped 10 mm from the bottom of the gel. The electrophoresis buffer used was 0.025 M Tris/0.192 M glycine, pH 8.3; bromophenol blue was used as tracking dye. The gel was fixed in 10% acetic acid/40% isopropanol/50% water for 60 min, stained with coomassie blue (0.05%) in 10% acetic acid/10% isopropanol/80% water for 60 min, and destained in 10% acetic acid/10% isopropanol/80% water, using three or four changes of solution over a 24-hr period.

Only qualitative differences were examined in this study, and only the faster migrating proteins were used, since alkaline PAGE is not the preferred method for resolving differences in basic (globulin-like) proteins, due to their short migration distances. The

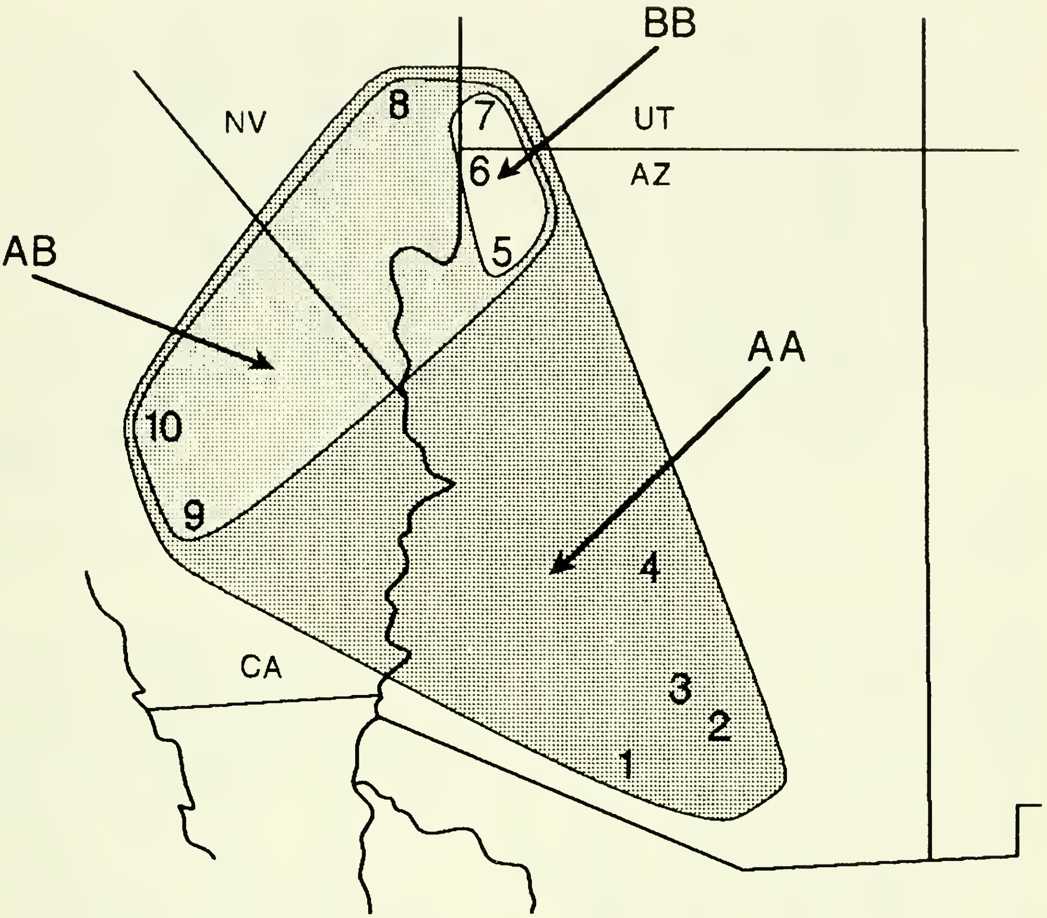

Fig. 1. Distribution of collection localities of tortoise genotypes AA, BB, and AB listed in Table 1. Numbers indicate localities.

electrophoretic mobilities of rattlesnake (*Crotalus atrox*) plasma albumin and bovine serum albumin were used as markers and compared with the albumin-like protein(s) of the desert tortoise samples. Both albumin markers migrated at faster rates than the tortoise albumin-like proteins analyzed in this study.

Genetic Analysis

Two protein loci, identified in order of decreasing anodal mobility, were designated "general proteins" (GP) 1 and 2. Allelic data at both loci were recorded as individual genotypes for analysis with the BIOSYS-1 program of Swofford and Selander (1981). Measures of genetic variability computed for each population sample included average locus heterozygosity (H, direct count) and the mean number of alleles per locus (A). The genetic distance and similarity coefficients of Nei (1972, 1978) and Rogers (1972) were calculated for all pairwise combinations of samples (corrected for small samples sizes as described by Levene [1949]), and all such matrices were clustered by the UPGMA algorithm of Sneath and Sokal (1973). Genotype ratios from the largest samples (localities 6 and 7, n = 12 for both) were tested for conformance to Hardy-Weinberg proportions by the X^2 goodness-of-fit option of BIOSYS, again corrected for small sample sizes (Levene 1949).

RESULTS

Sixty-eight individual samples were analyzed from four states, including 11 localities

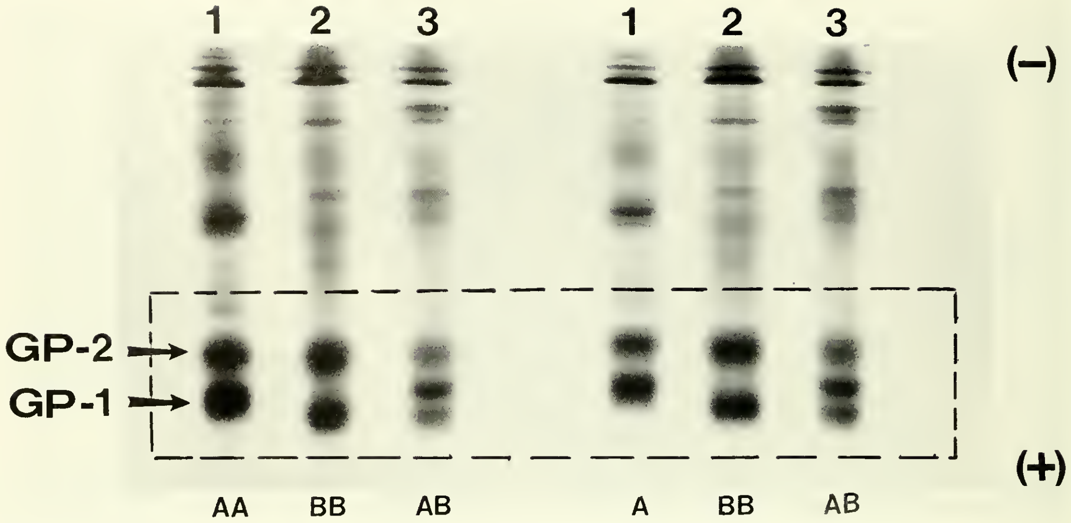

Fig. 2. Alkaline polyacrylamide gel illustrating GP-1 and GP-2 loci (enclosed in dotted rectangle), with allelic variation at GP-1 locus for plasma samples from three individuals (run in duplicate). Animals 1, 2, and 3 were consistently scored as genotypes AA, BB, and AB, respectively.

TABLE 2. Matrix of genetic distance coefficients of Nei (1978, above diagonal) and Rogers (1972, below diagonal) for all pairwise combinations of *Xerobates agassizi* localities; locality numbers are as listed in Table 1 and D values are rounded off to two decimals.

Locality	1	2	3	4	5	6	7	8	9	10
1	—	0.00	0.00	0.00	0.03	0.01	0.17	0.00	0.05	0.06
2	0.00	—	0.00	0.00	0.03	0.01	0.17	0.00	0.05	0.06
3	0.00	0.00	—	0.00	0.03	0.01	0.17	0.00	0.05	0.06
4	0.00	0.00	0.00	—	0.03	0.01	0.17	0.00	0.05	0.06
5	0.17	0.17	0.17	0.17	—	0.00	0.00	0.00	0.00	0.00
6	0.08	0.08	0.08	0.08	0.08	—	0.08	0.00	0.00	0.01
7	0.27	0.27	0.27	0.27	0.10	0.19	—	0.01	0.00	0.00
8	0.13	0.13	0.13	0.13	0.04	0.04	0.15	—	0.00	0.00
9	0.19	0.19	0.19	0.19	0.02	0.10	0.08	0.06	—	0.00
10	0.18	0.18	0.18	0.18	0.01	0.10	0.09	0.05	0.01	—

(considered as separate populations). The protein profiles present in 7 of 9 plasma samples from the Desert Tortoise Natural Area (CA) and 2 samples from Utah were unique but were very likely artifacts due to their badly hemolyzed condition. These 11 samples were excluded from the data analysis. This reduced the number of samples to 57 and the number of localities to 10 (Table 1). General protein-1 was polymorphic for two electromorphs (designated A and B) in several samples (Fig. 2). Table 1 summarizes the ratios of GP-1 genotypes across these 10 localities and the estimates of variability across both loci. Genotype ratios at localities 6 and 7 conformed to Hardy-Weinberg expectations ($X^2 = 2.789$, $P = .095$; $X^2 = .503$, $P = .478$, respectively, df = 1 in both cases), suggesting that this is a simple Mendelian co-dominant system with two alleles segregating in some populations. Table 2 summarizes pairwise comparisons of two genetic distance coefficients (Rogers 1972, Nei 1978) and shows that between-sample divergence was minimal. Nei's D values, for example, range from 0.00 to 0.17. Four of the Arizona samples (Maricopa Co., Pinal Co., Pima Co., and Tucson) are identical (Nei's D = 0.00). Five localities having the B allele at GP-1 formed a distinct separate cluster, albeit the total degree of divergence from the monomorphic populations was slight (D = 0.05). Within this group, the Arizona and California populations were nearly identical, while the Paradise Canyon (UT) samples were

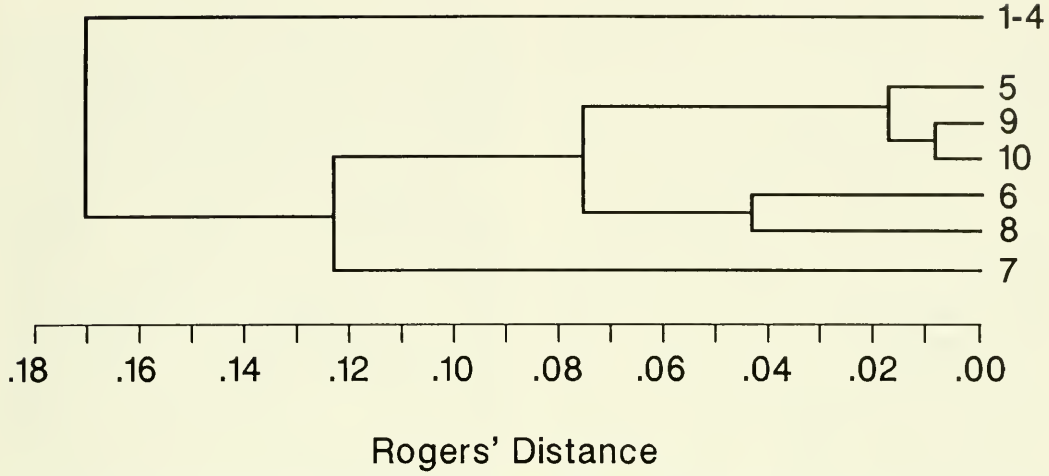

Fig. 3. Dendrogram based on Rogers' (1972) genetic distance values for 10 samples of *Xerobates agassizi* (see Table 1, Fig. 1). Clustering was by the UPGMA algorithm of Sneath and Sokal (1973), and the cophenetic correlation value was 0.826.

the most divergent. These relationships are also visually displayed in the UPGMA dendrogram presented in Figure 3, using the statistical analysis method of Rogers (1972). All other UPGMA dendrograms gave identical or nearly identical topologies (data not shown).

DISCUSSION

Dessauer (1970) reported that while some blood proteins in reptiles are relatively conservative, others are quite polymorphic. Many species can be readily distinguished by the electrophoretic mobilities of blood proteins, and certain subspecies and populations can also be distinguished by differences in plasma albumin-like proteins (Dessauer and Fox 1958, Masat and Dessauer 1968). Masat and Dessauer (1968) also found that the albumin-like proteins of the Testudines have slower migration rates in alkaline buffers than do these same proteins in most other reptiles (and mammals). We also found that under alkaline conditions the desert tortoise albumin-like proteins migrate at slower rates than rattlesnake plasma albumin and bovine serum albumin.

The results of this investigation suggest geographical differences in genetic variability of the albumin-like protein (GP-1) of desert tortoises. The northern (Mohavean) populations were polymorphic, whereas the southern (Sonoran) populations were monomorphic at the GP-1 locus. An east-west Mohave difference was observed due to the eastern isolation of the BB genotype (Table 1, Fig. 2) in populations from the eastern Mohave region of Utah and northwestern Arizona (Fig. 1). The B allele was not present in any of the central and southern Arizona samples. Those samples expressing the B allele may differ in the frequency of this allele, as suggested by the differentiation between Paradise Canyon and the Beaver Dam Slope, but the present sample sizes are too small for accurate determination. Despite the small sample sizes, the heterozygosity estimates are more similar for the Paradise Canyon population and the three Mohavean populations (8, 9, and 10) than for the Paradise Canyon and Beaver Dam Slope populations (Table 1). If the Paradise Canyon tortoises differ from the Beaver Dam Slope population(s) in frequency of the B allele and are in fact more similar to California tortoises, this could reflect: (a) a divergence of allele frequencies between the slope and Paradise populations in allopatry, with allele frequencies at Paradise simply drifting to values similar to California populations (similarity by convergence); (b) transport of tortoises from California or Nevada to St. George and "dumping" into Paradise Canyon, but not at the slope (i.e., human-induced gene flow between California, Nevada, and Paradise); or

(c) transport and release of Arizona tortoises (most with AA genotypes at the GP-1 locus) on the Beaver Dam Slope but not Paradise Canyon, which would cause the A allele at the slope to increase in frequency at the expense of the B allele and "push" the slope population away from Paradise Canyon and California allele frequencies (see genotype differences in Table 1). These are not mutually exclusive hypotheses since a certain amount of "mixing" may have occurred at all localities of California, Nevada, Beaver Dam Slope, and Paradise Canyon populations.

The long history of human collection and translocation of desert tortoises between states constitutes a variable that could influence the genetic structure of desert tortoise populations, especially when comparing allele frequencies between populations well known as captive release sites. Hundreds, perhaps thousands, of tortoises have been picked up along roadways and released in different regions over the past several decades (Mike Coffeen and Eric Coombs, UDWR, personal communication). This logistical displacement of tortoises continues at present. Certain localities have been popular release sites, e.g., regions of southern California (Desert Tortoise Natural Area), Arizona (McDowell Mountain region near Phoenix), Nevada (near Las Vegas and recreation areas), and Utah (St. George). The most common avenues of translocation by motorists crossing the Mohave Desert are east to west and vice versa. Favorable habitats for tortoises exist from Washington County in southwestern Utah to southern California—a region heavily traveled over a major interstate highway for decades. In addition to the release of tortoises in this region by motorists and local citizenry, Utah's Beaver Dam Slope population(s) have been the site of approximately 200 captive release tortoises, regulated by the Utah Division of Wildlife Resources since 1970 (Mike Coffeen, UDWR, personal communication).

Although Utah's tortoise populations located east of the Beaver Dam Mountains are often regarded as "captive escapees" in a nonindigenous setting, there are no scientific data confirming this view. The hypothesis seems to have originated from several sources, e.g., magazine and newspaper articles, and the opinions of a few naturalists and herpetologists. Support for the introduced status is based on three general observations. One is the fact that some tortoises found in the St. George region obviously have been captive specimens, exhibiting rope or chain holes in their shells or having painted areas on their shells. Second, residents of Washington County often keep tortoises as pets, and some have escaped or were purposely released. Third, the Beaver Dam and Virgin Mountains presently form an east-west barrier between natural assemblages, and a few reptiles found west of the mountains are not present east of them (e.g., *Crotalus scutulatus, Phyllorhynchus decurtus, Dipsosaurus dorsalis*). The possibility still remains that some of Utah's tortoises found east of the mountains may be derived from ancestral stock of naturally occurring tortoise populations that have since mixed with captive released specimens. Support for the natural population relies on the fact that the Mohave Desert Province extends into this region, and many other Sonoran life-zone animals found on the western slope are also found east of the mountains and are natural assemblages. Like the desert tortoise, some of the reptiles are life-zone specific and occur on both sides, for example, the banded gecko (*Coleonyx variegatus*), Gila monster (*Heloderma suspectum*), and sidewinder (*Crotalus cerastes*).

The geographical differences observed in this investigation are similar to those found in the allozyme survey by Jennings (1985), the mtDNA survey by Lamb et al. (1989), and the morphometric analysis of tortoise remains by Weinstein and Berry (1987). Specifically, the present study supports the earlier molecular investigations of Lamb et al. (1989), which showed divergence between tortoise populations north and west of the Colorado River and those to the south and east. Their report provided good evidence that tortoise populations now isolated on opposite sides of the Colorado River have likely been separated from each other for several million years. The mtDNA lineages from central and southern Arizona formed a single haplotype that differed from the northern haplotypes in CA, NV, UT, and extreme northwestern AZ by a minimum of 17 restriction site changes (see Fig. 2 in Lamb et al. [1989]). This is one of the highest levels of intraspecific genetic divergence reported for any animal species and exceeds that reported for many interspecific comparisons.

The exception in our study was the small sample from near Kingman, AZ (locality 5 in Fig. 1), which genotypically grouped with the Mohavean populations north and west of the Colorado River. Consequently, the genotypic composition for population 5 must be interpreted with caution. The single BB homozygote in a sample of three individuals would not be expected unless the B allele was segregating at a high frequency. These results may be due to several factors, e.g., the translocation of this specimen by humans, a sampling error for a low-frequency allele, or a degradational artifact in this sample. If future sampling verifies the presence of a high-frequency B allele at this locality, it could represent an ancestral polymorphism shared with Mohavean populations north of the Colorado River. This anomalous result underscores the need for statistically adequate sample sizes in all future genetic studies of the desert tortoise. Therefore, identifying the specific origin of any individual tortoise on the basis of nuclear gene markers may be difficult. Weinstein and Berry (1987) suggest using a combination of physiological and morphometric screening methods to designate regional types. They analyzed shell morphology of adult (> 180 mm) desert tortoises of both sexes by using morphometric data gathered by the Bureau of Land Management at 31 different localities. These measurements were collected from tortoise remains by several persons over a 48-year period. These authors noted that live tortoises were not used in their analysis and that shell morphology of tortoise remains does incur some shrinkage over time following death. They recommend further studies comparing live tortoises. None of these authors suggested that the differences observed in their investigations justify subspecific designation for any of the regional populations, and thus *Xerobates agassizi* remains a monotypic species.

Alkaline PAGE was useful in examining the albumin-like proteins in tortoise plasma but does not resolve slight differences in the electrophoretic mobility among the majority of the plasma proteins. However, this method did detect the polymorphic nature of the albumin-like (GP-1) protein, and this protein may be one "marker" that could be used for designation of broad regional types. Since the results of this investigation are, with the possible exception of locality 5 noted above, very similar to the findings of others in that the broad regional genotypes in desert tortoises are approximately concordant, the PAGE screening of the plasma protein marker may provide one inexpensive method of objectively determining the regional origin of tortoises. If allele frequency data are to be used, additional specimens from Paradise Canyon and Beaver Dam Slope populations are needed to determine the significance of the allele frequency differences between these two localities. Additional samples from throughout Nevada and California would also be required. Also, some variations observed in the slower-migrating proteins could be examined with more high-resolution techniques (e.g., isoelectric focusing, two-dimensional electrophoresis) combined with bio-image analytical instrumentation that can quickly and accurately scan and record qualitative differences in electrophoretic profiles. Morphometric data from live tortoises should be collected to compare Paradise Canyon and western slope populations in conjunction with future molecular analyses. In fact, external morphology (such as shell shape) could be a more functional criterion for the survivability of Paradise Canyon tortoises on the Beaver Dam Slope (see Weinstein and Berry [1987]), since genetic differences between these populations appear to be slight.

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EFFECTS OF NITROGEN AVAILABILITY ON GROWTH AND PHOTOSYNTHESIS OF *ARTEMISIA TRIDENTATA* SSP. *WYOMINGENSIS*

Paul S. Doescher[1], Richard F. Miller[2], Jianguo Wang [2], and Jeff Rose[2]

ABSTRACT.—This study examined the effects of alterations in soil nitrogen on the growth of *Artemisia tridentata* ssp. *wyomingensis* Nutt. Soil nitrogen content was altered by applying sugar (45 g/m^2), nitrate (4.5 g/m^2), or ammonium (4.5 g/m^2), and the results were compared with a control treatment (no soil amendments). Addition of either form of nitrogen significantly increased leaf nitrogen content, mean maximum length of ephemeral leaves, number of ephemeral leaves per terminal shoot, and current year's vegetative stem length over the control and sugar treatments. Both soil water and predawn xylem potentials during active growth were lower in the nitrogen-treated plots. The higher growth activity and greater leaf mass of *A. tridentata* in the nitrogen treatments may have been responsible for this result. Higher photosynthetic rates observed in the nitrogen treatments during an early June sampling period also lend support to this observation. This study suggests *A. tridentata* ssp. *wyomingensis* would opportunistically take advantage of increased availability of soil nitrogen. The ability of this species to respond positively to increased soil nitrogen may enhance its competitiveness over associated perennial species.

Artemisia tridentata Nutt. is a semideciduous perennial shrub occupying 44.8 million ha in the western Intermountain sagebrush-steppe. It is the most abundant shrub in this ecosystem. During the past century, increases of *A. tridentata* have been attributed to overgrazing of perennial grasses by domestic livestock, cultivation of lands too arid to produce crops, and alterations in fire frequency (Hironaka and Tisdale 1963, Tisdale et al. 1969, Tisdale and Hironaka 1981). As *A. tridentata* has increased in the Great Basin, both production and diversity of herbaceous understory species have declined. Numerous physiological and morphological characteristics of *A. tridentata* have been shown to enhance its effectiveness as a competitor with native bunchgrasses, especially for soil moisture (DePuit and Caldwell 1973, Eissenstat and Caldwell 1988, Miller and Shultz 1987, Miller 1988). Among these, the ability of *A. tridentata* to maximize leaf area early in the growing season by overwintering one-third of its leaf biomass and by developing ephemeral leaves early in the spring strongly enhances its ability to photosynthesize during favorable growth periods (Depuit and Caldwell 1973, Miller and Shultz 1987, Miller 1988). A deep, well-developed root system also allows *A. tridentata* to capture soil moisture from a soil volume much larger than that of perennial grasses (Sturges 1977).

Relatively little research has examined the response of this species to soil nutrients such as nitrogen. Limited work, however, indicates *A. tridentata* to be an effective competitor for soil nutrients. Caldwell et al. (1985) demonstrated that this species successfully competes for soil phosphorus with the native perennial grass *Agropyron spicatum* (Pursh) Scribn. & Smith. The accumulation of nutrients and higher soil nitrogen mineralization rates in surface soils beneath *A. tridentata* canopies may also convey an ecological advantage to plants during active growth periods (Charley and West 1975, 1977, Doescher et al. 1984). Few studies, however, have evaluated the response of *A. tridentata* to increased or decreased amounts of available soil nitrogen. Carpenter (1972), working in the Colorado Plateau, reported that 134 kg N/ha applied to *A. tridentata* yielded an 81% increase in total leafy material compared with a nontreated control. However, Carpenter and West (1987) found little response to nitrogen in *A. tridentata* grown on mine spoils. The form of nitrogen, whether NH_4 or NO_3, may also be an important factor in the mineral nutrition of aridland shrubs (Wallace et al. 1978).

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Our experiment was designed to determine how depletion or addition of different forms of nitrogen affects *A. tridentata* growth and carbon-assimilation rates. Our hypothesis was that *A. tridentata* responds favorably to increases in soil nitrogen.

Materials and Methods

The study was conducted at the Squaw Butte Experimental Range in southeastern Oregon (119°43′W longitude, 43°29′N latitude), 67 km west of Burns, on the northern fringe of the Great Basin. The 37-year mean annual precipitation for this area is 284 mm. Precipitation during the 1987 crop year (September–August) was 296 mm. The Squaw Butte Experimental Range typically receives most of its moisture between October and June, generally as snow, with little precipitation received in July and August. The mean temperature in winter is −0.6 C, with the daily minimum averaging −4.8 C, and the mean temperature in summer is 17.6 C, with the daily maximum averaging 26.8 C. The study site is located in an *Artemisia tridentata* spp. *wyomingensis*/*Stipa thurberiana* habitat type, at an elevation of 1,372 m (Doescher et al. 1984). This site has been excluded from grazing by domestic herbivores for the past 40 years. Soil texture is gravelly fine sandy loam and classified as Xerollic Durothids (Lentz and Simonson 1986). Soils vary in depth from 35 to 45 cm and are underlain by an indurated duripan 5–20 cm thick, which is underlain by unweathered basalt. A detailed description of soil nutrient levels is provided by Doescher et al. (1984).

Experimental Procedures

A completely randomized plot design was used with 10 replications of each treatment. Plots 5 × 5 m were laid out with an *A. tridentata* located in the center of each plot. To maximize uniformity, we selected plots that had vigorous-appearing *A. tridentata* plants of similar growth form and size. Plant measurements were recorded on the center *A. tridentata* plants, and soil measurements were collected within 1.5 m of the stem base. The remainder of the plot was used as a buffer.

Treatments were applied both in March and late November of 1986. Treatments were (1) control (no amendments added), (2) granulated sugar (45 g/m^2), (3) ammonium—$(NH_4)_2SO_4$ (nitrogen = 4.5 g/m^2), and (4) nitrate—HNO_3 (nitrogen = 4.5 g/m^2). Sugar addition was assumed to increase the C:N ratio to decrease availability of soil nitrogen (Baath et al. 1978). Both ammonium and sugar were broadcast onto the 5 × 5-m plots. Nitrate was diluted in water (1 part HNO_3 to 5 parts water) and applied with a backpack sprayer. All herbaceous plants were dormant at the time of application. Soil and plant growth measurements were recorded during the following 1987 growing season.

Soils were analyzed for ammonium and nitrate concentration in the A and B horizons in five plots per treatment on 14 April, 26 May, and 25 July. Soil analysis was performed using a KCl extracting technique (Horneck et al., in press).

Soil water content was measured from 1 April to 15 September once every two weeks in each of the A and B horizons. One soil sample was collected for each of the two depths within each plot for all treatments. Soil water was measured gravimetrically, and soil water release curves were developed for each depth to define soil water potential.

Ephemeral leaf number and maximum length, and vegetative stem elongation were measured on five randomly selected terminal branchlets of the single *Artemisia* located within each plot. Leaf measurements were recorded on three dates during initiation and expansion of ephemeral leaves (15 April to 5 May). Vegetative stem elongation was measured on five dates from initiation to termination of growth. Leaf nitrogen content was measured on current year's leaves (both ephemeral and persistent) collected from vegetative stems on 15 and 21 April, 1 June, and 1 August on all plots. Collections represented three phenological stages: initial leaf elongation, rapid leaf and stem growth, and early flowering. The Semimicro-Kjeldahl method was used to determine total leaf nitrogen content (Bremmer 1965). Specific leaf weight (g/m^2) was obtained by measuring leaf area on current year's green leaves on 12 dates during the growing season. Leaves were removed from one randomly selected terminal branch in each plot and placed in a damp cooler. Several hours later leaf area was measured on a leaf area meter, and weight was determined by oven-drying the leaves at 60 C for 48 hr.

TABLE 1. Soil nitrate and ammonium content (ppm) at soil depths of 0–20 cm and 20–40 cm.

	Treatment			
Sampling date	Control	Sugar	Nitrate	Ammonium
NO_3 0–20 cm				
April 14	0.50^{a*}	0.48^{a}	12.42^{b}	1.20^{a}
May 26	1.16^{a}	1.14^{a}	6.84^{a}	1.16^{a}
July 25	1.82^{a}	3.28^{a}	11.64^{b}	5.02^{ab}
20–40 cm				
April 14	0.74^{a}	0.84^{a}	20.60^{b}	1.64^{a}
May 26	1.56^{a}	1.10^{a}	8.46^{b}	1.46^{a}
July 25	1.62^{a}	1.90^{a}	9.02^{b}	3.46^{ab}
NH_4 0–20 cm				
April 14	6.32^{a}	4.18^{a}	5.14^{a}	7.78^{a}
May 26	4.92^{a}	4.82^{a}	7.22^{a}	4.92^{a}
July 25	0.80^{a}	0.70^{a}	3.00^{a}	0.70^{a}
20–40 cm				
April 14	7.88^{a}	6.82^{a}	10.18^{a}	12.32^{a}
May 26	8.96^{a}	7.68^{a}	11.04^{a}	11.96^{a}
July 25	1.04^{a}	1.10^{a}	2.84^{a}	9.30^{b}

*Numbers followed by the same letters are not significantly different ($P < .05$) between treatments for each soil depth and date.

Xylem potentials (Scholander et al. 1965, Waring and Cleary 1967) on current year's vegetative branchlets were measured during the 1987 growing season with a pressure chamber (PMS Corporation, Corvallis, Oregon). Predawn (19 May, 3 June, and 21 July) and midday (15 April and 3 June) measurements were recorded between 0430 and 0630, 1130 and 1230 hr, respectively. Five branchlets were measured in each treatment. Samples were selected at random, removed from the shrub, and immediately measured in the pressure chamber.

Photosynthesis was measured on one randomly selected vegetative branchlet of an *Artemisia* plant in 5 of the 10 plots for each treatment on eight dates from mid-April through early August. Measurements were recorded between 1200 and 1300 hr using a LI-6000 (LI-COR, Lincoln, Nebraska) portable photosynthesis meter with a quarter-liter chamber. To attain an adequate amount of leaf area in the chamber, we recorded measurements on both previous and current season vegetative branchlets. Initial photosynthesis values were used and corrected using the formula developed by LI-COR (McDermitt 1987).

Statistically significant treatment effects for variables measured on *Artemisia* were identified using analysis of variance procedures. Time was set as a variable, in addition to treatment. Least significant differences (LSD) ($P < .05$) were calculated only when the F value was significant ($P < .05$) (Steel and Torrie 1980). The General Linear Model Procedure of SAS was used to evaluate treatment differences for specific leaf weight and photosynthesis (SAS 1988). This procedure permitted statistical analysis of unbalanced data sets. Both interactions and main effect means were separated using Fischer's least significant difference test. Only statistically significant results are reported in the Results and Discussion.

RESULTS

Soil Nitrogen

The addition of nitrate increased nitrate levels 25- and 28-fold in the upper and lower soil depths, respectively, at the beginning of the growing season (Table 1). Nitrate levels remained high compared with the other three treatments at both depths during the growing season. The shallow character of the soil probably limited nitrate losses to leaching, maximizing the amount available for plant uptake. The addition of ammonium increased ammonium 188% in the B horizon. The increase in

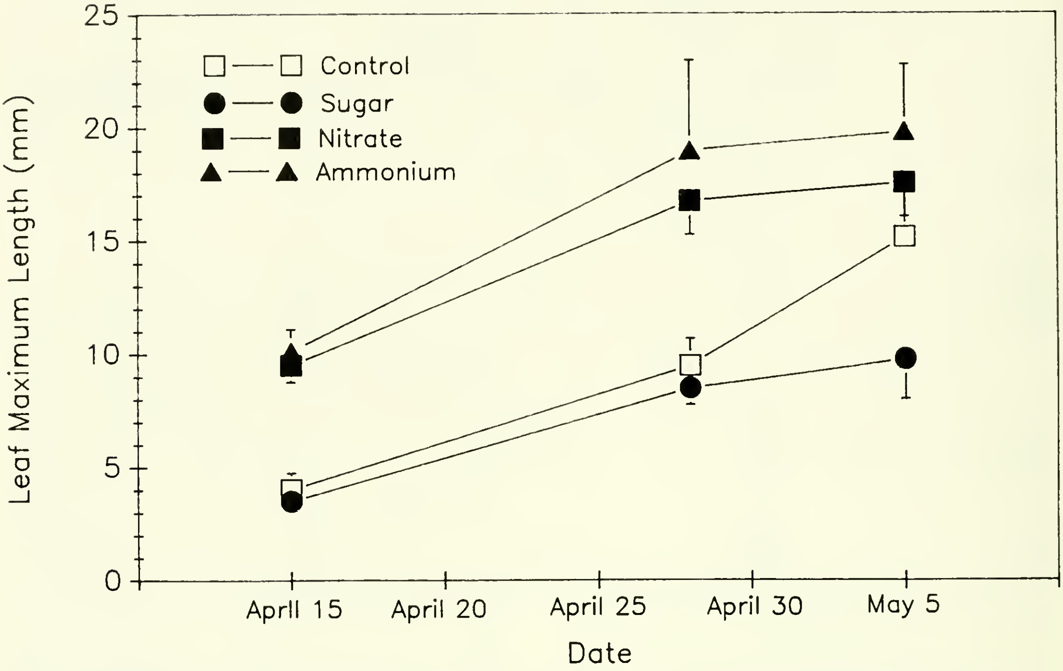

Fig. 1. Ephemeral leaf maximum length of *Artemisia tridentata* ssp. *wyomingensis* during the early growing season. Standard errors are presented for each mean.

the A horizon was not significant. The sugar treatment did not appear to change soil nitrogen levels when compared with the control, possibly indicating that carbon was not limiting decomposer microflora (McGarity 1961).

Growth

In the early spring both mean maximum length of ephemeral leaves and number of ephemeral leaves per terminal shoot were greater in the ammonium and nitrate treatments than in the sugar and control treatments (Figs. 1, 2). Ephemeral leaf lengths during April in the nitrogen-treated plots did not differ from one another but were greater than in the nonnitrogen treated plants. Control and nitrate-treated plants did not differ from one another in leaf length for the May sampling period. Analysis of main effect means for ephemeral leaf numbers revealed that plants in nitrogen-treated plots did not differ from one another, and that their values were greater than similar values found for the control and sugar treatments. In addition, the development of new leaves on terminal shoots in both nitrate and ammonium treatments appeared to increase at a greater rate in early May than in sugar and control plots.

The addition of nitrogen increased current year's vegetative stem length compared with no nitrogen addition throughout the growing season (Fig. 3). Stem length was similar between both nitrogen forms in April and May but continued at a more rapid rate in the nitrate treatment in June. At the termination of vegetative stem elongation, stems in the nitrate and ammonium treatments were 175 and 140% longer, respectively, than shoots in the control treatment. Stem elongation in the control and sugar treatments was similar.

The addition of either form of nitrogen did not increase specific leaf weight averaged across the growing season as compared with the control treatment (Table 2). The addition of sugar, however, reduced specific leaf weight across dates on the average by 12% compared with the control. The major difference in specific leaf weight between control and sugar treatments occurred during abscission of ephemeral leaves in late July and early August (Fig. 4). Specific leaf weight increased approximately 180 to 200% when ephemeral

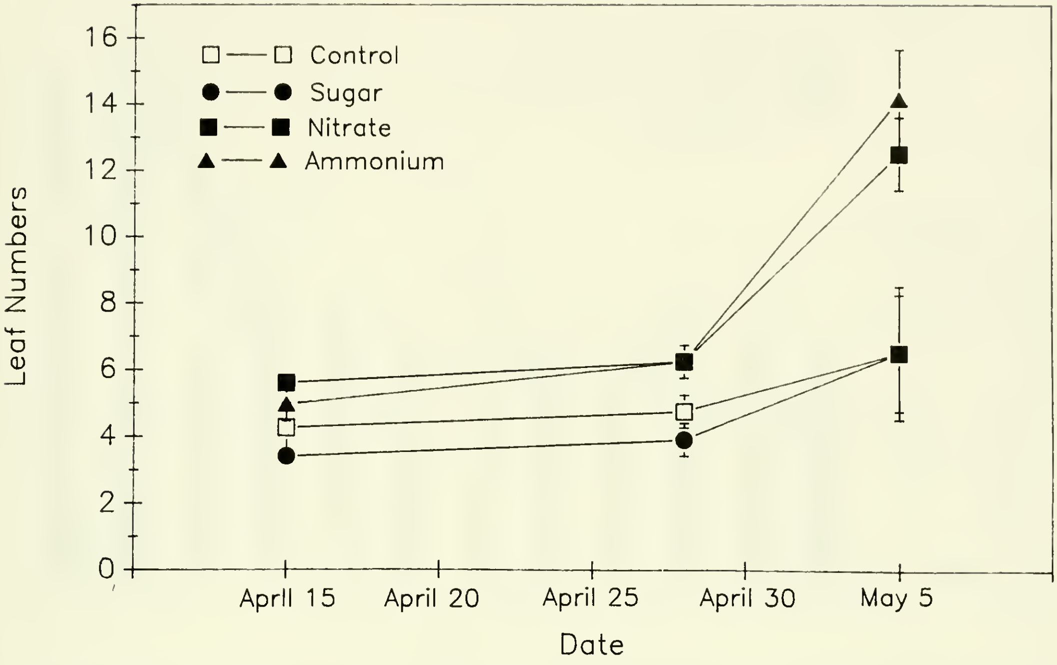

Fig. 2. Ephemeral leaf numbers per terminal bud of *Artemisia tridentata* ssp. *wyomingensis* during the early growing season. Standard errors are presented for each mean.

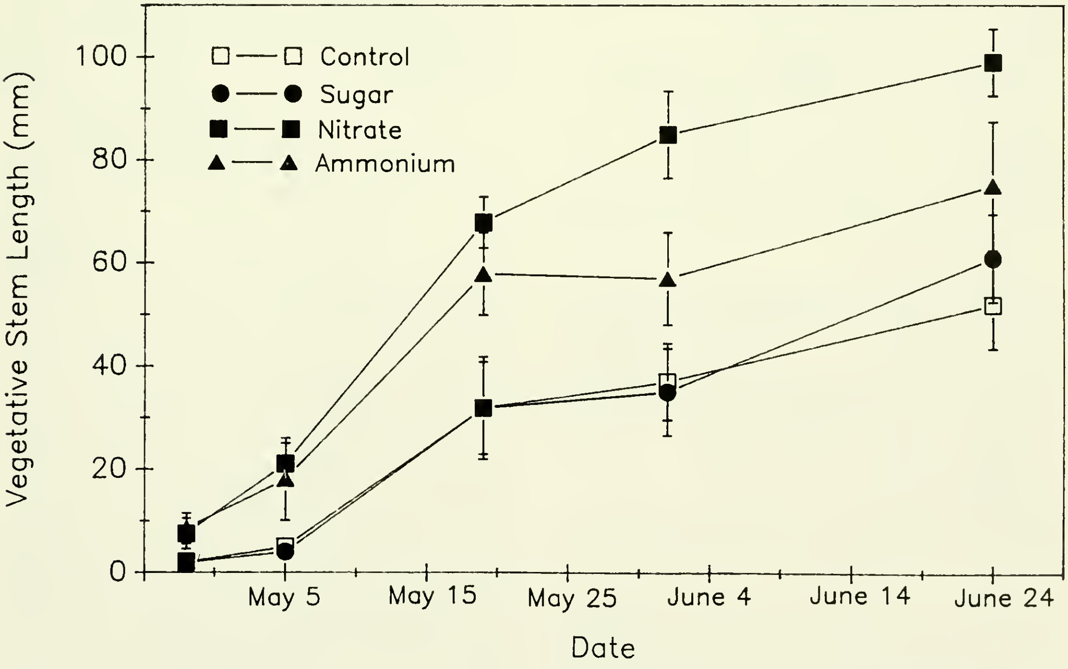

Fig. 3. Effects of four different nitrogen treatments on current year vegetative stem length of *Artemisia tridentata* ssp. *wyomingensis*. Standard errors are presented for each mean.

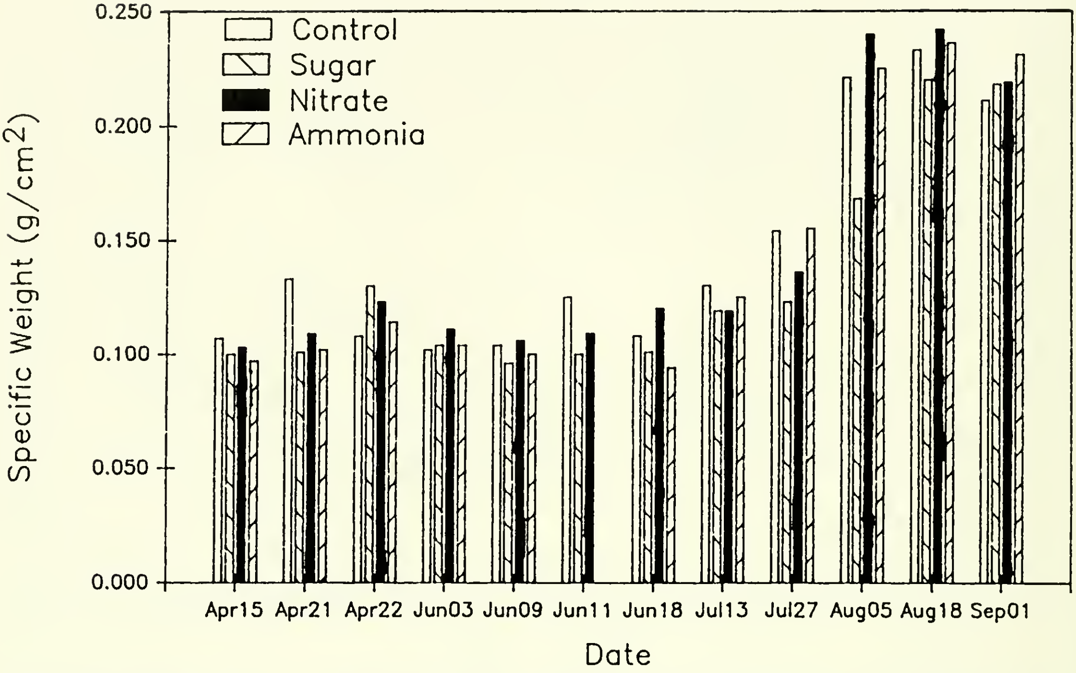

Fig. 4. Specific leaf weights of *Artemisia tridentata* ssp. *wyomingensis* during the course of the 1987 growing season.

TABLE 2. Specific leaf weights of *Artemisia tridentata* ssp. *wyomingensis* growing under four nitrogen treatments. Mean values are averaged over the 1987 growing season.

Treatment	Specific leaf weight (g/m^2)
Control	145^{a*}
Sugar	132^{b}
Ammonium	141^{a}
Nitrate	145^{a}

*Means followed by similar letters are not significantly different at $P \leq .05$.

TABLE 3. Leaf nitrogen concentration (mg/g) of *Artemisia tridentata* ssp. *wyomingensis* growing under four nitrogen treatments. Means are averaged over the 1987 growing season.

Treatment	Leaf nitrogen concentration (mg/g)
Control	19.6^{a*}
Sugar	19.6^{a}
Ammonium	25.1^{b}
Nitrate	27.0^{b}

*Means followed by similar letters are not significantly different at $P \geq .05$

leaves abscised in August for all treatments. By late August, when most ephemeral leaves had abscised, specific leaf weight between treatments was similar.

Application of both forms of nitrogen resulted in greater leaf nitrogen contents of *Artemisia* plants (Table 3). Analysis of main effect means revealed that plants in the nitrate and ammonium treatments had greater concentrations than did the control and sugar treatments.

Water Relations and Photosynthesis

Soil water depletion rates were generally more rapid in the nitrogen-treated plots at both soil depths than in the sugar and control plots (Figs. 5, 6). Differences were greatest during rapid growth in mid-May in the lower 20 cm. In the upper 20 cm, the sugar-treated plots maintained the highest soil water content from April through May.

Predawn plant water potentials were similar among treatments in mid-May and late July (Table 4). During rapid growth in June, however, predawn plant water potentials in nitrogen-treated plots were lower than both control and sugar treatments. Midday water potentials were also lower in June in both nitrogen treatments compared with sugar and control. Both predawn and midday readings declined in all treatments as the season progressed.

Photosynthesis was significantly different between treatments on only the 15 June 1987

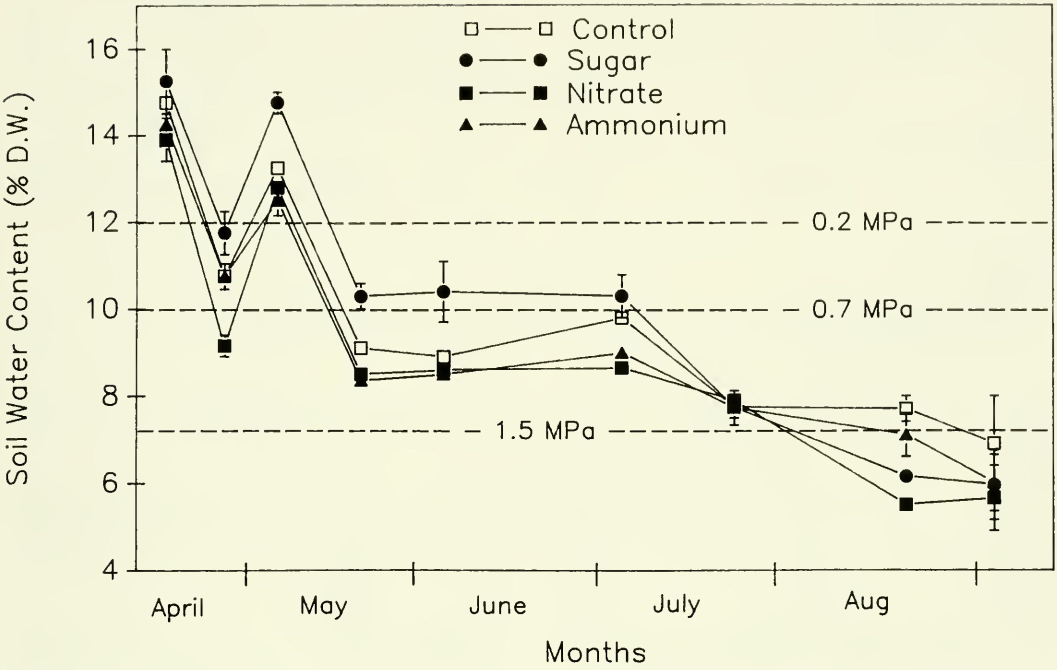

Fig. 5. Seasonal pattern of soil water content in the upper soil profile (2–20 cm) for four different nitrogen treatments in 1987. Vertical bars are 95% confidence limits. Field capacity (−0.03 MPa) = 18% soil water content.

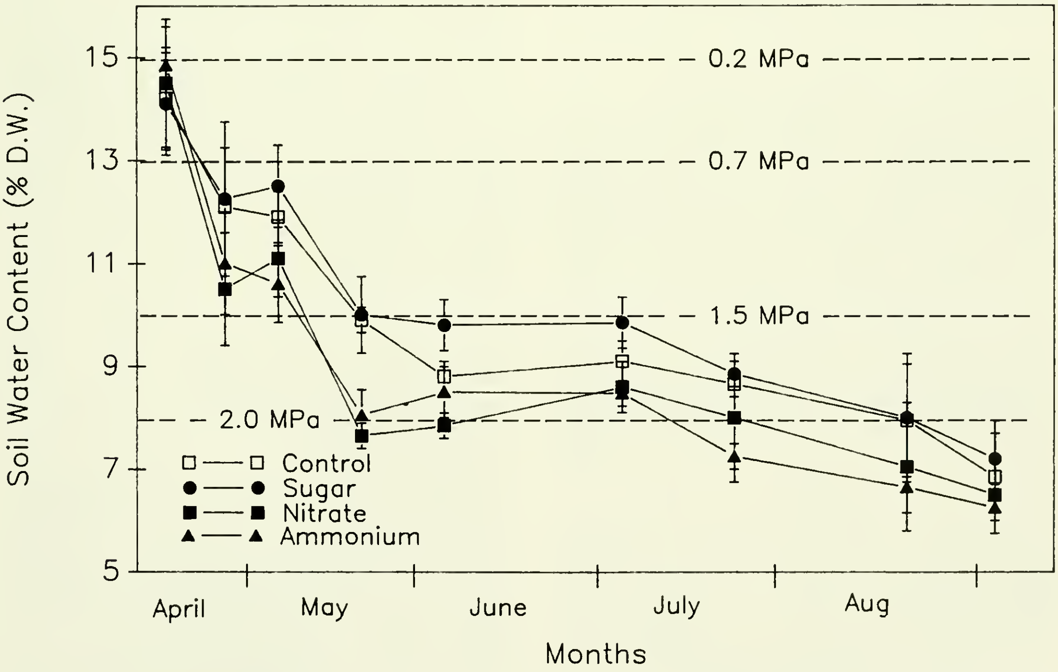

Fig. 6. Seasonal pattern of soil water content in the lower soil profile (20–40 cm) for four different nitrogen treatments in 1987. Vertical bars are 95% confidence levels.

TABLE 4. Predawn and midday plant water potentials (MPa) in *Artemisia tridentata* ssp. *wyomingensis* through the growing season in 1987.

	Treatments			
Date	Control	Sugar	Nitrate	Ammonium
Predawn				
May 19	-1.24^{aA*}	-1.05^{aA}	-1.04^{aA}	-1.21^{aA}
June 3	-1.31^{aA}	-1.44^{bA}	-1.77^{bA}	-1.77^{bB}
July 21	-1.62^{bA}	-1.62^{bA}	-1.74^{bA}	-1.77^{bA}
Midday				
April 15	1.85^{aA}	-1.67^{aB}	-1.65^{aB}	-1.62^{aB}
June 3	-2.09^{bA}	-2.06^{bA}	-2.24^{bB}	-2.31^{bB}

*Numbers followed by the same lowercase letters are not significantly different ($P < .05$) between dates for each treatment, numbers followed by the same uppercase letters are not significantly different ($P < .05$) between treatments for each site.

TABLE 5. Photosynthesis (mg $CO_2 \cdot m^{-2} \cdot sec^{-1}$) of *Artemisia tridentata* ssp. *wyomingensis* under four nitrogen treatments during 1987.

Date	Control	Sugar	Nitrate	Ammonium
April 17	0.30^{*}	0.00^{a}	0.36^{a}	0.54^{*}
June 15	0.25^{b}	0.33^{b}	1.73^{a}	2.18^{a}
June 20	0.20^{b}	0.16^{a}	0.28^{a}	0.25^{a}
July 30	0.42^{a}	0.22^{a}	0.22^{a}	0.20^{a}
August 1	0.43^{a}	0.43^{a}	0.20^{a}	0.51^{a}

*Means followed by the same letter are not significantly different between treatments at the same date.

date (Table 5). Increased photosynthesis on this date corresponded to the period of rapid leaf and stem growth in early June.

DISCUSSION

Nitrogen availability is probably second only to water as the most limiting factor to biomass production in Great Basin plant communities (James and Jurinak 1978). At our study site, addition of nitrogen was also found to significantly promote aboveground growth of *A. tridentata* ssp. *wyomingensis*. Fertilization increased ephemeral leaf size, number of ephemeral leaves, and stem elongation rates. Fertilization also increased nitrogen amounts in the subsoil and the leaves. These responses lend support to our original hypothesis, namely, that *A. tridentata* responds favorably to increases in soil nitrogen.

Although our results showed a positive growth response in *A. tridentata* to nitrogen, the role nitrogen plays in influencing growth of arid species is poorly understood. In the desert Southwest, researchers have reported a variable response of *Larrea tridentata* (DC.) Cov.–dominated communities to water and nitrogen inputs (Gutierrez and Whitford 1987, Fischer et al. 1987). During certain years, application of water and/or nitrogen resulted in enhanced growth, while in other years no response was observed. Fischer et al. (1987) concluded this variable response was due to yearly changes in available soil nitrogen. In the Great Basin, biomass production of forage species has not always been related to precipitation (Charley 1972, Sneva and Britton 1983, Miller et al. 1990). Sneva and Britton (1983) and Miller et al. (1990) reported reduced herbaceous production in the third of three consecutive wet years. It has been speculated that nitrogen may be limiting following successive wet years, as prolonged plant growth depletes soil nutrients and poor quality organic matter is slow to decompose (Parker et al. 1984, Fischer et al. 1988). On a reclaimed mine spoil, Carpenter and West (1987) indicated no response to nitrogen additions for the species *Artemisia tridentata* ssp. *vaseyana*. Available nitrogen was probably not limiting due to stockpiling of topsoil and the lack of site occupation by an establishing plant community. In Carpenter and West's (1987) study leaf nitrogen concentration of control plants was 3.2%. In contrast, our study had leaf nitrogen concentrations of 2.0, 2.7, and 2.5%, for control, nitrate, and ammonium, respectively. Site and subspecies differences may have also contributed to the different response.

A positive growth response was shown for the ammonium plots in spite of enhanced ammonium levels being found only in the 20–40 cm soil depth. The nonsignificant concentrations of ammonium in the surface soils may have been caused by losses due to volatilization, absorption of ammonium on soil colloids, high biological activity, and/or ammonium being hydrolyzed to nitrate in the lower soil depth. Also, the growth response may have been related to the application of ammonium in the sulfate form. Whether or not *A. tridentata* responds to sulfur additions has yet to be determined. Despite the lack of enhancement in the upper soil depth of the ammonium-treated plots, the extensive root system of *A. tridentata* would allow this species to readily utilize ammonium in the lower soil depths.

Xylem potential and soil moisture readings found in this study would, at first, appear contradictory to the observed growth responses. The more negative soil moisture and plant water potentials reported for *A. tridentata* growing in the nitrogen plots suggest that these plants were more water stressed, and thus should have reduced aboveground growth. However, the opposite was found. We feel that a possible explanation for these results centers on the greater growth and physiological activity of plants in the nitrogen plots. Since specific leaf weights were similar between treatments during active leaf growth, we can assume that differences in leaf area between treatments are approximately proportional to biomass. Leaf biomass of *A. tridentata* in the nitrate and ammonium plots was found to have increased 520 and 230%, respectively, over control (Wang 1989). Greater growth and leaf area of these plants may mean that more soil water was used by plants in the nitrogen treatments. This observation is supported by the research of Svejcar and Browning (1988). They reported a greater leaf area, higher physiological activity, and a subsequently more rapid soil water depletion in burned versus unburned stands of *Andropogon gerardii* Vitman. The greater photosynthetic rates of *A. tridentata* in the nitrogen plots during early June also further support this observation. In addition, an increase in shoot-to-root ratio could have influenced plant-water relations. Nitrogen additions have been reported to increase shoot-to-root ratios in *Larrea tridentata* (Fischer et al. 1988, Lajtha and Klein 1988).

Specific leaf weights averaged across the growing season were significantly influenced by the sugar treatment. Prior to leaf senescence, specific leaf weights were similar between treatments on seven of eight dates measured. Specific leaf weights in the sugar treatment, however, were significantly less than in the control during senescence and abscission of current year's ephemeral leaves. Once the majority of ephemeral leaves had abscised in mid-August for all treatments, specific leaf weights were again similar. The decrease in specific leaf weights in the sugar treatment was probably a function of delayed leaf senescence and abscission rather than leaves being lighter per unit of surface area. Although not indicated by the soil nitrogen data, some reduction in available soil nitrogen may have occurred on the sugar plots.

Marschner (1986) reported an increase in leaf area indices in plant populations with an increase in nutrient supply. Increased leaf development during the early part of the growing season and a larger leaf area index in the years when mineralizable nitrogen levels are relatively high may increase *Artemisia*'s competitive advantage for nutrient resources over associated species. Miller (1988) reported that *Artemisia* maintained a relatively high leaf area early in the spring compared with associated species, allowing it to capture soil water resources early in the growing season. Early increased leaf area also enhances its ability to maximize photosynthesis when environmental conditions are favorable (DePuit and Caldwell 1973). In warm desert shrubs, rate of leaf area development was the primary factor limiting whole-plant carbon gain during the early portion of the growing season (Comstock et al. 1988).

In conclusion, application of both nitrate and ammonium increased growth response of *A. tridentata* over control and sugar treatments. Apparently this species can opportunistically take advantage of increased soil nitrogen by increasing amount of leaf area available for growth. Increases in available soil nitrogen might occur following events such as several consecutive years of below-average precipitation or weakening of perennial grasses through overgrazing. *A. tridentata* may enhance its competitiveness by responding favorably to increased levels of soil nitrogen.

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FORM AND DISPERSION OF MIMA MOUNDS IN RELATION TO SLOPE STEEPNESS AND ASPECT ON THE COLUMBIA PLATEAU

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ABSTRACT.—Patterned ground consisting of Mima-type earth mounds and associated sorted stone circles and nets is widespread on the Columbia Plateau of western North America. Studies of the geometric relationships of mounds and stone nets to slope aspect and steepness were carried out at the Lawrence Memorial Grassland Preserve, north central Oregon, in June 1987. Mound and moundfield characteristics were sampled on randomly chosen 1-ha plots on slopes of different aspect and steepness. Mounds were largest, most circular and symmetrical in form, and most fully encircled by beds of size-sorted stones on level sites. On slopes of increasing steepness, mounds decreased in size, showed increasing asymmetry and downslope elongation, and became connected into lines oriented up- and downslope. Encircling stone beds became more weakly developed or disappeared on upslope and downslope sides of the mounds, and the lateral beds developed downslope extensions that eventually merged with those of adjacent upslope and downslope mounds. These patterns are interpreted as reflecting changes in the manner of soil translocation by northern pocket gophers, *Thomomys talpoides*, due to their responses to tunneling on slopes and to the modification of the flow of water across the slope because of the presence of mounds.

Mima-type earth mounds are a characteristic feature of grasslands with shallow soils or poor drainage in western North America (Cox 1984). These mounds, containing stones up to about 50 mm in diameter, commonly range up to 2 m in height, 20 m in diameter, and 50 ha^{-1} in density. Recent investigations at several locations have supported the hypothesis that Mima-type mounds are formed over long periods of time by the centripetal translocation of soil toward centers of activity of geomyid pocket gophers. These centers, located initially in the deepest, best drained sites available, are gradually transformed into mounds by soil translocation (Cox 1984, Cox and Allen 1987b, Cox and Gakahu 1987, Cox et al. 1987).

Mima mounds are an extensive and prominent feature of the shrub steppe of the Columbia Plateau in eastern Washington, northern Oregon, and southwestern Idaho, USA. Here the mounds are frequently encircled by beds of sorted stones, and intermound flats often exhibit polygonal networks of sorted stone beds (Waters and Flagler 1929, Kaatz 1959, Malde 1961, 1964, Fosberg 1965). These features, formerly interpreted as periglacial features, have also been interpreted as a result of soil translocation by pocket gophers (Cox and Allen 1987a).

Our previous studies of Mima mounds and sorted stone beds have been conducted on level areas where mounds are circular in form and regular in spacing. Observations by previous workers (cited above) and patterns evident on aerial photographs indicate that mound form and moundfield geometry are modified considerably on slopes. The objective of this study was to define variation in mound form and moundfield geometry with slope aspect and steepness, and to determine if the activities of pocket gophers can account for the variation.

METHODS

Studies were conducted at the Lawrence Memorial Grassland Preserve (LMGP) and on adjacent ranch land of the Priday Brothers Corporation, southern Wasco County, Oregon (44°57′N, 120°48′W), 1–11 June 1987. This was the site of previous studies of the structure of mounds and associated beds of sorted stones (Cox and Allen 1987a, Cox et al. 1987). The LMGP, a registered national landmark owned by the Nature Conservancy, lies at an elevation of 1,036–1,060 m on the Shaniko Plateau, formed of Columbia River basalts, and includes several ravines that fall steeply northward into the valley of Ward Creek, 122 m below. The preserve has a cold, semidesert climate with an average annual precipitation of 280 mm. The surface of the plateau is mounded "biscuit scabland" with Mima mounds that range up to about 2 m in height and 20 m in diameter. The mound soils are classed as Condon eolian silt loams, and the intermound soils as Bakeoven residual very cobbly loams. The vegetation of mounds and deeper upland soils is dominated by Idaho fescue (*Festuca idahoensis*) and bluebunch wheatgrass (*Agropyron spicatum*). The shallow intermound soils are dominated by scabland sagebrush (*Artemisia rigida*), Sandberg bluegrass (*Poa scabrella*), several species of biscuitroot (*Lomatium* spp.), and bitterroot (*Lewisia rediviva*). The northern pocket gopher (*Thomomys talpoides*) is abundant throughout the preserve. A comprehensive physical and biotic inventory of the LMGP is given by Copeland (1980).

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Relationships of mound and moundfield characteristics to slope and aspect were explored by sampling mounds throughout the LMGP and on a small area of adjacent ranch land. For this sampling, an aerial photo with a superimposed 100 × 100-m grid was used. Some grid units that included very steep slopes or canyon bottoms were largely or entirely unmounded. Since the objective of the study was to examine mound characteristics in relation to slope, only mounded grid units (> 50% of the surface showing mound-intermound topography) were considered for sampling. This criterion also assured that the grid units selected were internally uniform in their slope. These grid units, with the aid of a topographic map, were also grouped tentatively into five aspect classes: level (with an overall slope less than 2.5°), or north-, east-, south-, or west-facing. All grid units within the 153-ha LMGP were considered. In addition, to allow adequate representation of south-facing slopes, a 10-ha area of land north of Ward Creek was also included. Sets of 7 grid units were chosen by random coordinates in each of the five aspect classes (a total of 35 grid units).

The aerial photo was then used to locate these grid units (hereafter termed plots) in the field. The overall aspect of each plot was determined with a compass and the slope steepness measured with an inclinometer. A count of the mounds in each plot was obtained, and the mound nearest the plot center was designated for detailed measurements. Maximum mound height was measured with a meter stick and line level. The orientation of the long axis of the mound (downslope direction) was measured with a compass. Maximum and minimum diameters were measured with a meter tape, and the components of these diameters relative to the highest point on the mound were also recorded (mound top to upslope edge, top to downslope edge, etc.). Distances to the first and second nearest neighbors (between mound high points) were also measured with a meter tape, as was the minimum distance between the highest points of the two mounds that were furthest apart in this three-mound set. The fraction of the mound encircled by beds of bare, size-sorted stones (Cox and Allen 1987a) was recorded for the upslope and downslope halves of the mound. The length of stone beds diverging from that surrounding the mound and extending downslope ("tails") was recorded. The maximum length of this measurement was the point at which this "tail" reached another mound. Finally, the number of discrete pocket gopher activity areas was recorded as an estimate of the number of animals occupying the mound. Areas with surface heaps or plugged tunnel openings were considered separate activity areas when they were separated by more than 5 m.

From these measurements a number of descriptive characteristics were calculated. Mound area was calculated assuming that the base was a circle or ellipse, and volume was computed on the assumption that the mound was a segment of a sphere or prolate spheroid. Elongation (E1) was computed from the following relationship:

$$\mathrm{E1} = \sqrt{(a^2 - b^2)}/a$$

where *a* and *b* are the major and minor radii. A second measure of elongation (E2) was also calculated as the ratio of the major to minor diameters of the mound. Asymmetry (AS) was calculated

$$\mathrm{AS} = [(1 - Sl)^2 + (1 - Ss)^2]^{0.5}$$

where *Sl* and *Ss* are the asymmetries on the

TABLE 1. Characteristics of Mima mounds and moundfields on plots differing in slope steepness at the Lawrence Memorial Grassland Preserve, north central Oregon. Values are means ± standard errors.

		Slope steepness (°)			
Characteristic	Overall (n = 35)	0–2.5 (n = 6)	2.5–5.0 (n = 15)	5.0–7.5 (n = 8)	7.5–10.0 (n = 6)
Mound features					
Height (cm)	68.7 ± 2.8	81.7 ± 6.8	67.9 ± 4.4	62.9 ± 5.1	65.7 ± 6.5
Area (m^2)	145.9 ± 14.6	188.0 ± 25.1	174.9 ± 24.7	118.2 ± 26.2	68.0 ± 8.9
Volume (m^3)	52.8 ± 6.2	78.6 ± 13.7	60.6 ± 10.1	40.6 ± 11.2	23.5 ± 5.3
Elongation	1.42 ± 0.11	1.23 ± 0.18	1.46 ± 0.20	1.73 ± 0.20	1.07 ± 0.11
Asymmetry	0.59 ± 0.08	0.14 ± 0.04	0.59 ± 0.08	0.78 ± 0.23	0.77 ± 0.27
Sorted stone beds					
Upslope side (%)	36.6 ± 5.6	59.2 ± 17.1	35.3 ± 7.8	34.4 ± 13.1	20.0 ± 8.2
Downslope side (%)	25.8 ± 4.9	45.8 ± 16.6	28.0 ± 7.5	17.5 ± 7.0	11.7 ± 7.9
Overall (%)	31.5 ± 4.7	52.5 ± 15.6	31.7 ± 6.3	25.9 ± 9.5	17.5 ± 7.7
Downslope tails (m)	2.17 ± 0.64	0	1.65 ± 0.73	4.89 ± 2.13	2.02 ± 1.11
Moundfield features					
Density (ha^{-1})	21.6 ± 1.2	18.8 ± 2.3	21.5 ± 1.9	24.4 ± 3.1	21.2 ± 2.9
Connection	0.11 ± 0.03	0.05 ± 0.05	0.18 ± 0.06	0.04 ± 0.04	0.09 ± 0.06
Linearity	0.84 ± 0.02	0.74 ± 0.06	0.88 ± 0.03	0.77 ± 0.06	0.91 ± 0.03
Mounded surface (%)	31.5	35.3	37.6	28.8	14.4

long and short axes, respectively, calculated

$$Sl = a'/a \qquad Ss = b'/b$$

where a' and b' are the longer, and a and b the shorter distances from mound edge to peak along the major and minor axes. Connection (C) of the sampled mound to the two nearest mounds on opposite sides was calculated as the mean of ratios of heights of between-mound divides to maximum mound height. Linearity (L) of alignment of the sampled mound and its two nearest neighbors was determined as the ratio of the sum of distances measured from center to center for a series of mounds to the single straight-line distance between the first and last in the sequence.

Data on mound and moundfield characteristics were analyzed by BMDP statistical software procedures (Dixon 1983). Logarithmic and arc-sine transformations were employed to achieve normality for some variables. Means and standard errors were computed for plot data grouped by slope aspect and slope steepness classes, and these classes were then compared by t-tests and ANOVA (BMDP 1D and 7D). Correlations among all combinations of variables and stepwise linear regressions using selected variables as the dependent variable were also performed (BMDP 2R).

Plant names follow Hitchcock and Cronquist (1973).

RESULTS

Measurements of the overall slope aspect in the field revealed that several of the plots tentatively placed in particular aspect classes actually fell in other classes. As a result, the final set of samples comprised 10 N-facing, 5 E-facing, 5 S-facing, and 8 W-facing plots (Table 1).

Mound and moundfield characteristics showed a complex relationship to slope aspect and steepness. With respect to slope steepness, mounds at the LMGP were confined to slopes less than about 10° in steepness. Mounds exhibited greatest height, basal area, and volume on level areas or very gentle (< 2.5°) slopes (Table 1). Basal area and volume declined progressively with increased slope steepness (ANOVA, $F_{3,31} = 3.62$, $P < .05$ for area; $F = 3.29$, $P < .05$ for volume). The mean height of mounds on level to very gently sloping areas was significantly greater than on steep (5.0–7.5°) slopes ($t = 2.26$, $DF = 12$, $P < .05$). Volume, the best overall indicator of mound size, showed a strong negative correlation ($r = -.496$, $P < .01$) with slope steepness (Fig. 1).

Mound asymmetry and elongation were both greatest on steep (5.0–7.5°) slopes (Table 1). Asymmetry was significantly lower for mounds on level to very gently sloping

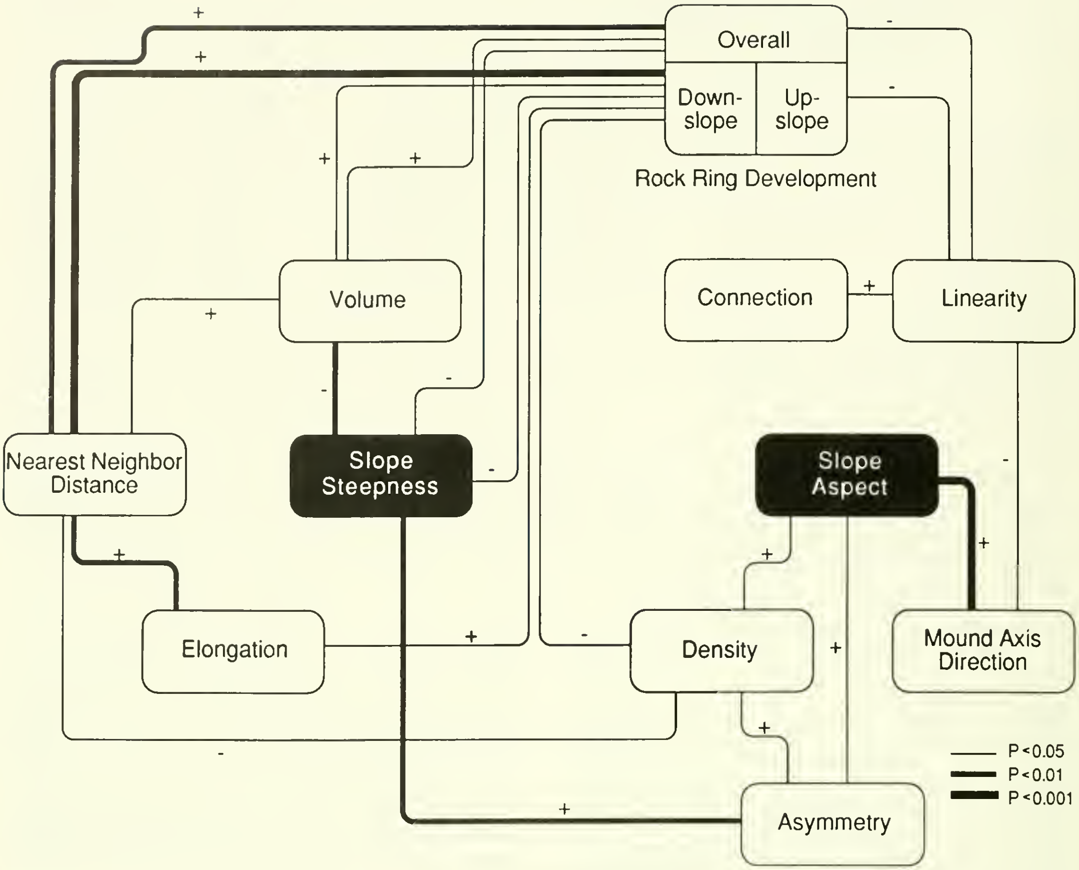
+
+
Overall
Down-slope
Up-slope
Rock Ring Development
+
+
Volume
+
Connection
+
Linearity
-
-
Nearest Neighbor Distance
Slope Steepness
-
Slope Aspect
-
+
+
+
Elongation
+
-
Density
+
Mound Axis Direction
+
-
+
Asymmetry
P<0.05
P<0.01
P<0.001

Fig. 1. Correlation relationships between major variables of mound and moundfield geometry for plots sampled on slopes of differing steepness and aspect at the Lawrence Memorial Grassland Preserve, north central Oregon, June 1987.

(0–2.5°) areas than on gentle (2.5–5.0°) slopes ($t = 3.30$, $\mathrm{DF} = 19$, $P < .01$), steep slopes ($t = 2.35$, $\mathrm{DF} = 12$, $P < .05$), or very steep (7.5–10.0°) slopes ($t = 2.33$, $\mathrm{DF} = 10$, $P < .05$). Asymmetry was also strongly correlated ($r = .449$, $P < .01$) with slope steepness (Fig. 1). Elongation, defined as the ratio of long to short mound axis, was significantly greater on steep slopes than on level to very gently sloping areas ($t = 3.07$, $\mathrm{DF} = 12$, $P < .01$). Elongation was significantly greater on steep than on very steep slopes ($t = 2.56$, $\mathrm{DF} = 12$, $P < .05$).

The development of encircling beds of bare, size-sorted stones was strongest on level to very gently sloping plots (Table 1), the degree of overall development being negatively correlated ($r = -.343$, $P < .05$) with slope steepness (Fig. 1). The negative correlation between the development of sorted stone beds and slope steepness was stronger on the downslope side of mounds ($r = -.367$, $P < .05$) than on the upslope side ($r = -.304$, $P > .05$).

Moundfield characteristics showed weaker patterns. Density of mounds showed little variation with slope steepness (Table 1). Connection and linearity, which were positively correlated ($r = .343$, $P < .05$), exhibited highest values on steeper slopes. Linearity was significantly lower on level to very gently sloping (0–2.5°) plots than on plots with gentle (2.5–5.0°) slopes ($t = 2.29$, $\mathrm{DF} = 19$, $P < .05$) or very steep (7.5–10.0°) slopes ($t = 2.28$, $\mathrm{DF} = 10$, $P < .05$). The combination of mound size (basal area) and density resulted in a greater surface coverage by mounds on very

TABLE 2. Characteristics of Mima mounds and moundfields on plots differing in aspect at the Lawrence Memorial Grassland Preserve, north central Oregon. Values are means ± standard errors.

Characteristic	Overall (n = 35)	Aspect Level (n = 7)	North (n = 10)	East (n = 5)	South (n = 5)	West (n = 8)
Mounds						
Height (cm)	68.7 ± 2.8	80.7 ± 5.8	75.6 ± 4.4	60.0 ± 8.0	54.2 ± 5.4	63.9 ± 5.2
Area (m^2)	145.9 ± 14.6	172.3 ± 26.4	146.6 ± 24.5	117.1 ± 42.3	121.0 ± 42.4	155.2 ± 39.2
Volume (m^3)	58.2 ± 6.2	71.5 ± 13.6	57.1 ± 11.1	40.7 ± 18.3	30.7 ± 8.4	52.1 ± 15.6
Elongation	1.42 ± 0.11	1.10 ± 0.20	1.32 ± 0.20	1.72 ± 0.32	1.60 ± 0.18	1.51 ± 0.28
Asymmetry	0.59 ± 0.08	0.15 ± 0.03	0.51 ± 0.08	1.00 ± 0.34	0.66 ± 0.30	0.75 ± 0.14
Rock circles						
Upslope side (%)	36.6 ± 5.6	50.7 ± 16.7	33.5 ± 11.5	41.0 ± 18.6	38.0 ± 10.7	24.4 ± 6.2
Downslope side (%)	25.8 ± 4.9	39.3 ± 15.4	20.5 ± 10.5	20.0 ± 10.5	25.0 ± 12.2	25.0 ± 11.3
Overall (%)	31.5 ± 4.7	45.0 ± 15.2	27.0 ± 9.1	30.5 ± 13.5	31.5 ± 10.3	25.9 ± 6.1
Rock tails (m)	2.17 ± 0.64	0	1.95 ± 1.06	4.64 ± 3.25	3.28 ± 1.63	2.11 ± 1.03
Moundfield features						
Density (ha^{-1})	21.6 ± 1.2	17.8 ± 2.2	20.0 ± 1.3	23.6 ± 4.1	26.8 ± 5.0	22.5 ± 2.6
Connection	0.11 ± 0.03	0.09 ± 0.06	0.20 ± 0.09	0.06 ± 0.06	0.08 ± 0.08	0.06 ± 0.04
Linearity	0.84 ± 0.02	0.78 ± 0.06	0.91 ± 0.03	0.75 ± 0.09	0.82 ± 0.04	0.86 ± 0.04
Mounded surface (%)	31.5	30.7	29.3	27.6	32.4	34.9

gentle to gentle slopes than on steep to very steep slopes.

Data for mounds grouped by slope aspect (Table 2) indicate that mound size (height, basal area, volume) was greatest on level plots and next greatest in height and volume on north-facing slopes. Mounds were smallest in both height and volume on south-facing slopes and next smallest on east-facing slopes. The variation among heights on plots differing in aspect was significant (ANOVA, $F_{4,30} = 3.48$, $P < .05$). Mean volume on south-facing slopes was significantly less than on level sites ($t = 2.31$, $DF = 10$, $P < .05$).

Mounds were least elongate or asymmetric on level and north-facing plots, and most elongate and asymmetric on east-facing slopes (Table 2). Elongation, expressed as the ratio of longer to shorter axis, was significantly greater for east- and south-facing plots than for level plots ($t = 3.14$ and 2.76, respectively, for east- and south-facing plots, $DF = 10$, $P < .05$). Variation in asymmetry was significant among aspect groups (ANOVA, $F_{4,30} = 3.29$, $P < .05$). Elongation of mounds was closely parallel to slope, the long axis of the mound being very highly correlated with the slope direction (Fig. 3, $r = .822$, $P < .001$). The development of sorted stone circles differed little for slopes of differing aspect (Table 2). Downslope tails of sorted stones were noted on slopes of all aspects.

Mound density was positively correlated with slope aspect, expressed as deviation in degrees from north ($r = .405$, $P < .05$). Density ranged from 17.8 mounds ha^{-1} on level plots to 26.8 mounds ha^{-1} on south-facing slopes (Table 2). Linearity of a sample mound and its two nearest neighbors was greatest for north-facing and least for east-facing slopes. Linearity was significantly greater for north-facing slopes than for level plots ($t = 2.26$, $DF = 15$, $P < .05$).

Several other important relationships were not directly linked to either slope steepness or slope aspect (Fig. 1). A number of these centered on nearest neighbor distance and stone circle development. Nearest neighbor distance was positively correlated with mound volume ($r = .349$, $P < .05$). In addition, nearest neighbor distance showed a strong, direct correlation with mound elongation ($r = .449$, $P < .01$) and stone circle development ($r = .468$, $P < .01$). Furthermore, the correlation of nearest neighbor distance to development of the stone circle on the downslope side of mounds was very strong ($r = .641$, $P < .001$). Mound volume also showed a direct relationship to stone circle development, both overall ($r = .346$, $P < .05$) and on the downslope side ($r = .415$, $P < .05$). The more elongate a mound, the greater was the development of the stone circle on its downslope side ($r = .379$, $P < .05$). The greater the density of mounds, however, the poorer was the development of the stone circle on the downslope side of the mound (r = −.423, P < .05). Linearity of mound arrangement, on the other hand, was negatively related to development of the stone circle, both overall (r = −.339, P < .05) and on the upslope side (r = −.335, P < .05). Finally, density showed a positive correlation with asymmetry (r = .364, P < .05), and mound axis direction was negatively correlated with linearity of mound arrangement (r = −.335, P < .05).

Discussion

The major patterns of variation of mound and moundfield characteristics with slope steepness and aspect are listed below.

1. Mounds show maximum size, circular and symmetrical form, low connection and linearity, and well-developed stone circles on level sites.
2. On slopes, mounds become smaller and more elongate and asymmetrical, with the long axis parallel to the slope, and show greater connection and linearity of arrangement.
3. On slopes, stone circles become weaker, especially on the downslope side of mounds, and stone beds diverge to form downslope tails.
4. Slope effects are, in general, more intense on south- and east-facing slopes than on north- and west-facing slopes (except for connection, which tends to peak on gentle north-facing slopes).

Much variation exists in the literature concerning the steepness of slopes on which mounds occur. Waters and Flagler's (1929) data on the Columbia Plateau and nearby areas record mounds on slopes up to only 6° in steepness, and Kaatz (1959) stated that mounds occur on slopes up to about 7° in steepness. Brown (1951), however, reported that mounds in this region occur on slopes up to 35–45°. Vitek (1973) reported mounds in southern Colorado on mountain slopes up to 20° in steepness, and in southern California, Cox (1984) found mounds on slopes up to 30° in steepness. Price (1949) stated that mounds occur in the western states in mountain meadows with slopes up to 20–30°. This variation in maximum steepness of mounded slopes may be real and may relate to soil texture and other factors affecting vulnerability to erosion. Mounds may occur only on slopes of 20° steepness or greater when soils are rich in clays, as they are in many locations in southern California (Cox 1984).

Researchers also offer diverse statements on how mound shape varies with slope steepness. Scheffer (1958) states that Mima mounds are "generally circular in shape as seen from above, regardless of slope." Vitek (1973), in southern Colorado, found that mounds tend to be nearly circular even on slopes up to 10.4° in steepness. On the Columbia Plateau, however, mounds are usually described as being more elongate on slopes. In southern Washington and northern Oregon, Waters and Flagler (1929) reported that the mean ratio of major to minor axes increases with increasing slope to a value of 1.43 on slopes of 6° steepness. The long axis of these mounds is said to be parallel to the slope. Malde (1964) noted that mounds in southwestern Idaho are typically circular, but that on hillsides they are noticeably elliptical, with the long axis directed downslope. Kaatz (1959), in central Washington, found that the typical mound is elliptical in shape, with a ratio of major to minor axis of about 1.41, the long axis being parallel to the slope. Olmsted (1963) found that mounds in eastern Washington are often elongate, the ratio of major to minor axis being 1.1–1.5. He also stated that the long axis is aligned with prevailing winds and is sometimes across slopes rather than parallel to them. Fosberg (1965) stated that in Twin Falls County, Idaho, mounds elongate into downslope stripes.

A degree of connection, or confluence, of mounds and their alignment into rows parallel to the slope has been noted by several workers. Waters and Flagler (1929), Malde (1964), and Fosberg (1965) describe mounds on the Columbia Plateau as forming beadlike rows along small drainage divides or between stone stripes on steeper slopes. Perhaps the best overall description of this pattern, together with that of mound form, is given by Brown (1951) for sites near Maupin, Oregon:

> On the steeper slopes they are oriented in more or less parallel lines along the rill divides, tend to be elongate and coalesce and are not as high nor as perfectly kept up as on the level. Looking at these slopes from a distance

> or studying aerial photos, one gains the impression of a continuous mound down the slope as though it constituted the entire rill divide. A close inspection, however, reveals that the crest of the strip is not even, that it is divided by well formed mounds rising above the level of the surrounding soil.

Fewer authors describe changes in the arrangement of sorted stone beds as slope steepness increases. Malde (1961, 1964) states that in southwestern Idaho the stone pavements surrounding mounds change progressively to parallel stone stripes running up- and downslope, implying the disappearance of pavement sections on the up- and downslope edges of mounds. Kaatz (1959), stating that stone circles and networks change to sorted stone stripes on steep slopes, also notes that sorted stripes may occur without any upslope connection to the former features. Brunnschweiler (1962) describes a similar pattern and diagrams a configuration in which stone "tails" arise from stone rings encircling mounds, or from intermound polygonal networks, to extend downslope. Pyrch (1973) noted that sorted stone stripes occur on slopes up to a maximum steepness of 15–33°. At the LMGP, Cox and Allen (1987a) found that on level areas the development of stone circles is directly correlated with mound size, and that on slopes the initial pattern of modification is the weakening of the bordering bed on the downslope side of the mound and the divergence of downslope "tails."

Are these mound features compatible with the basic hypothesis of origin of both mounds and associated stone circles, polygonal nets, and stripes by the soil translocation activities of pocket gophers? And if so, how does this mechanism interact with site characteristics related to steepness and aspect to yield the observed patterns?

Let us first consider the implications of the relationship of the intensity of moundward soil translocation by pocket gophers to distance from the center of a small mound and elevation below its top, as observed by Cox and Allen (1987b). For a mound on a level site, average moundward translocation increased with distance from the mound center, and average upward translocation increased with elevation below the mound top. On a level site these tendencies would be distributed symmetrically, other factors being equal, and the mound would tend to enlarge symmetrically, maintaining a circular shape.

For a similar small mound on a slope, however, differences in translocation would result even if the amount of tunneling activity remained the same in terms of distance and direction from the mound center. On the sides of the mound lying on the slope contour, moundward and upward translocation will be similar to soil movements on a mound on level ground. On the downslope side of the mound, however, an animal must move soil a greater vertical distance to achieve the same horizontal displacement. Since this requires greater energy expenditure, horizontal displacement will probably often be less than expected. On the upslope side of the mound, in contrast, a given horizontal displacement will occur with less vertical displacement. In some cases, of course, much of the actual horizontal displacement will be downslope. Thus, expenditure of the same energy will lead to a greater than expected horizontal displacement.

The consequence of differences in mean displacement distance is that more soil will be translocated onto the upslope side of the mound than onto the downslope or lateral sides. The mound should thus grow most in a lateral and upslope fashion. However, this growth could permit a circular form to be retained as long as the average of upslope and downslope addition rates equals the addition rates to the lateral edges of the mound. Such a pattern will prevail whenever the mean horizontal translocation distance of soil at a given distance from the mound center is linearly related to the mean slope of the translocation path (Fig. 2).

If the relationship of mean displacement distance to slope is curvilinear and convex, however, then additions to the lateral edges will be greater than expected, and to the upslope and downslope edges less than expected; thus, the mound will expand in width (across the slope). If the relationship is curvilinear and concave, additions to the upslope and downslope edges will be greater than expected, and those to the lateral edges less than expected; the mound will elongate up- and downslope. In the latter case, the total amount of soil translocated onto the downslope side of the mound will still be much less than that moved onto the upslope surface. As the mound grows in height, addition to the downslope side of the mound will also decline. At the same time, slope conditions on

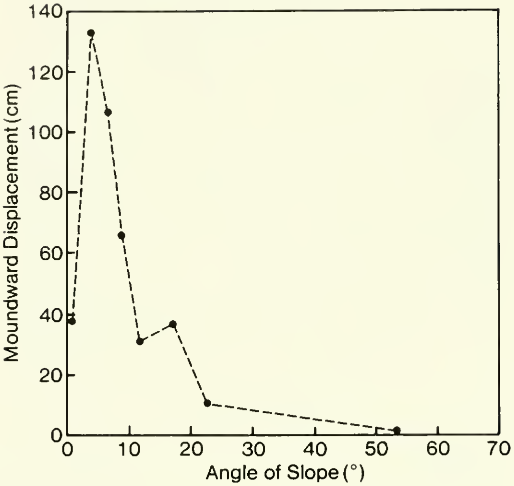

Fig. 2. Horizontal displacement distance (moundward) for soil mined by *Thomomys bottae* in southern California in relation to slope for data from Cox and Allen (1987b).

the upslope side of the mound will still permit heavy translocation onto the mound surface. Thus, slope relationships should cause erosional loss of soil to balance moundward translocation sooner on the downslope side of the mound than on the upslope side. Upslope growth should therefore continue after downslope growth has stopped.

Data from soil translocation studies of *Thomomys bottae* in southern California (Cox and Allen 1987b) suggest that soil translocation by pocket gophers of this genus varies with steepness in a curvilinear, concave fashion over a range from less than 5° to more than 50° (Fig. 3). These data were obtained in studies of soil translocation on level sites, where the only slope was that of the mounds themselves.

Elongation of mounds on the Columbia Plateau should be coupled with an upslope movement of the mound high point. At maximum size, the highest point of an elongated mound should thus be nearest its upslope end.

Elongation of mounds should lead to connection with adjacent mounds up- and downslope when the soil mantle is deep enough to permit the development of large mounds. Such connection may create a linear, "beaded" arrangement of mounds parallel to the slope. This arrangement will give a strong measure of linearity if the two nearest neighbors of a given mound are upslope and downslope in the connected line. Strong linearity of arrangement on a slope would thus imply that the mean distance between mounds in the same line is less than that between mounds in different lines. This should not be the case if uniformly spaced mounds develop on a slope and those directly up- and downslope from each other become connected. Our data show only a weak relationship between slope steepness and linearity, suggesting that little more than the connection of mounds lying up- and downslope from each other has occurred.

The presence of a mound on a slope would modify the flow of water across the slope, concentrating it along the upper and lateral sides of the mound and producing a dry shadow downslope (Cox and Allen 1987a). The concentrated flow of water along the sides of a mound would tend to continue directly downslope. These areas of maximum wetness favor the formation of sorted stone beds extending downslope. Several possible mechanisms may contribute to the transformation of beds encircling the mounds into elongate stripes paralleling them. Growth of fleshy-rooted plants may lead to extensive tunneling by pocket gophers in these areas. The collapse of deep tunnels and the downward settling of soil and small stones during the wet season may thus sort and expose stones near the surface (Cox and Allen 1987a). Erosion may also play an important role, particularly as slope steepness increases.

Figure 4 diagrams a hypothesis of how circular, isolated mounds surrounded by sorted stone nets become transformed into elongate, interconnected mounds bordered by linear beds of sorted stones. This hypothesis predicts that lines of mounds on slopes should be separated by two stone stripes, one representing the fusion of downslope extensions of the encircling beds of each line of mounds. Examination of aerial photos of sloping areas on the LMGP shows that this is generally true. These observations strongly support the overall hypothesis that pocket gophers interact with physical conditions and processes to produce the distinctive patterns of mounds and sorted stone beds on the Columbia Plateau.

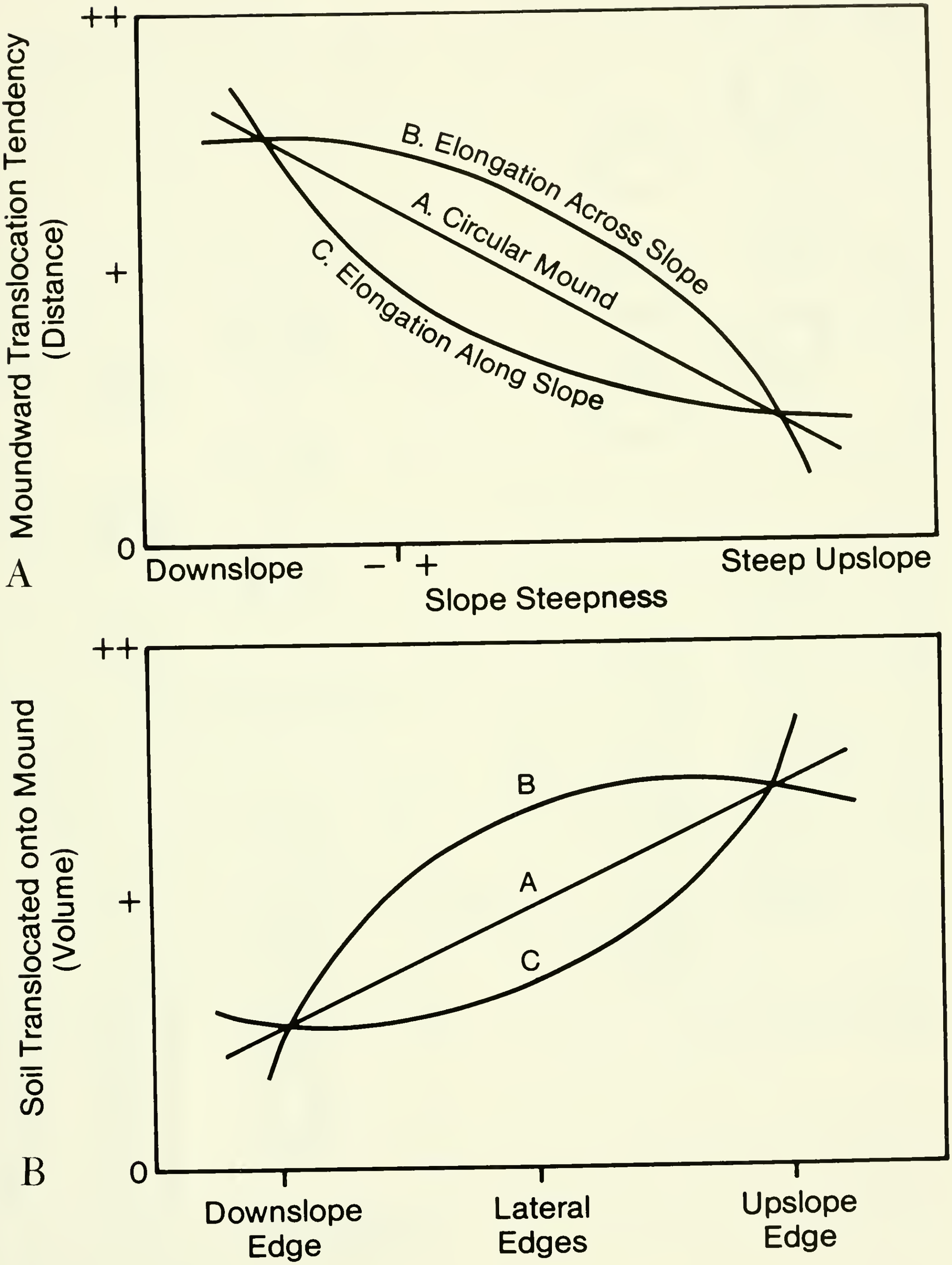

Fig. 3. (A) Possible relationships between mean horizontal translocation distance (moundward) and slope steepness. (B) Volume of soil moved onto mound surface at various points around mound perimeter by pocket gopher translocation in relation to slope steepness, based on the relationships outlined in (A) for a mound of a given slope.

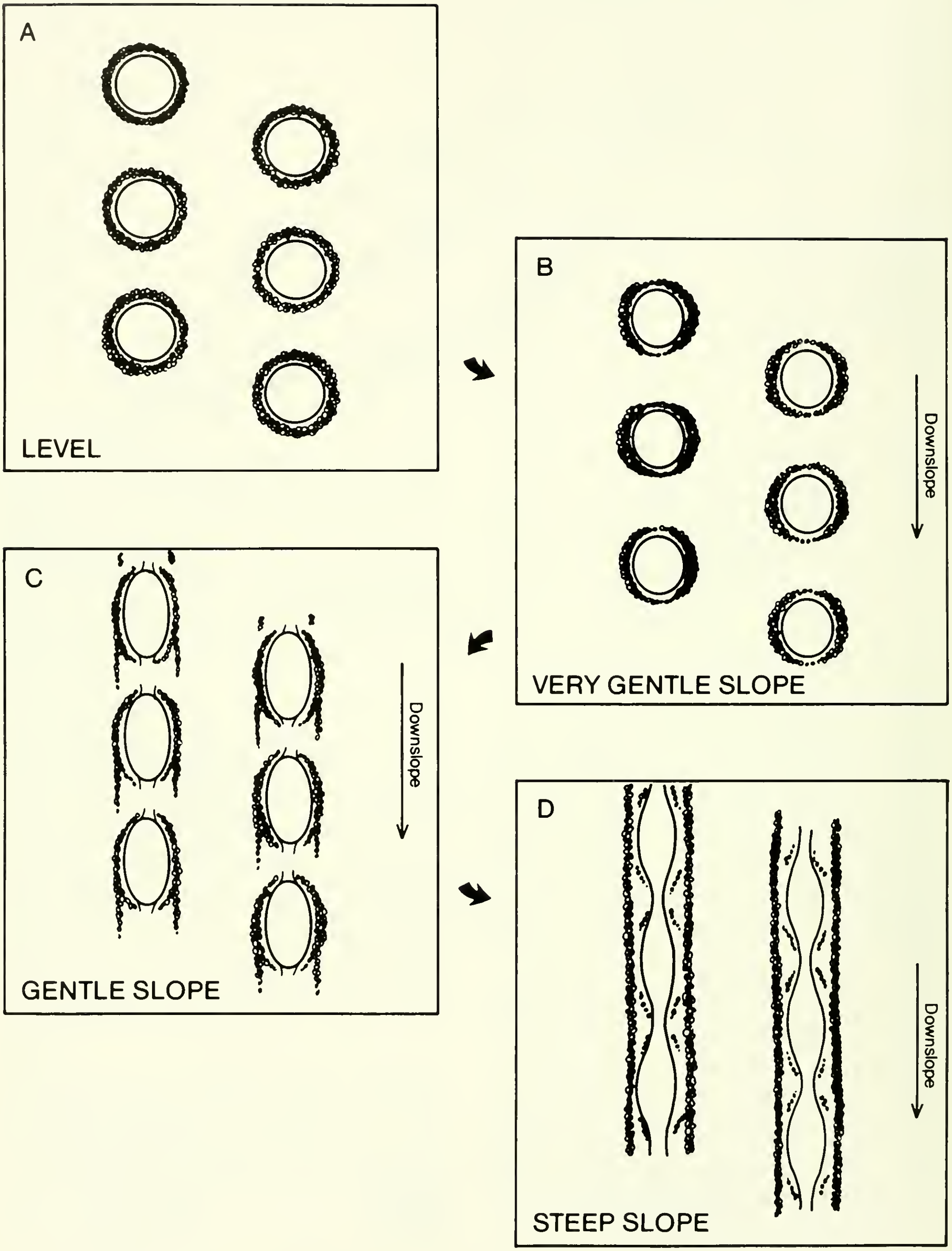
A
LEVEL
B
VERY GENTLE SLOPE
Downslope
C
GENTLE SLOPE
Downslope
D
STEEP SLOPE
Downslope

Fig. 4. Diagrammatic model of the transition of unconnected, circular mounds with encircling stone rings on level sites to linearly connected, elongate mounds bordered by stone stripes on steep slopes.

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ESOX LUCIUS (ESOCIDAE) AND *STIZOSTEDION VITREUM* (PERCIDAE) IN THE GREEN RIVER BASIN, COLORADO AND UTAH

Harold M. Tyus[1] and James M. Beard[1,2]

ABSTRACT.—Northern pike, *Esox lucius*, stocked in the Yampa River in 1977, invaded the mainstream Green River by 1981 and subsequently increased in range and abundance. The speed of this invasion is indicated by two recaptured pike that moved 78 and 110 km, respectively, downstream in about one year. Pike stomachs (n = 123) were usually empty (54.5%), but some contained fish (43%) and nonfish items (2.4%). Red shiner, *Notropis lutrensis*, and fathead minnow, *Pimephales promelas*, predominated among the 12 fish species eaten. Walleye, *Stizostedion vitreum*, presumably introduced to the Green River drainage in the 1960s, was widely distributed but low in abundance. Most of 61 adult walleye stomachs contained food (60.7%); of 6 fish species eaten, channel catfish, *Ictalurus punctatus*, and fathead minnow were most frequently consumed. Northern pike and walleye were captured in habitats occupied by endangered Colorado River fishes, particularly Colorado squawfish, *Ptychocheilus lucius*. Predation on endangered fishes was not detected, but northern pike and walleye consumed at least three other native fishes. The northern pike may pose a threat to endangered fishes due to its population expansion, piscivory, and resource sharing. Diets of northern pike and walleye species should be further evaluated if their abundance increases.

Northern pike were introduced into Elkhead Reservoir, an impoundment on the Yampa River drainage, in 1977 (P. J. Martinez, personal communication) and collected in the mainstream Yampa River as early as 1979 (E. J. Wick, personal communication). Their numbers increased in the upper Yampa River in the early 1980s (Wick et al. 1985), and a downstream movement into the Green River was subsequently documented in 1981 (Tyus et al. 1982, Green River fishery investigations). Northern pike reproduction has been reported in the upper Yampa River drainage, where it has access to the mainstream river (T. P. Nesler, personal communication).

Walleye presumably accessed the mainstream Green River by moving downstream from various tributaries. The fish was first reported in Utah in 1951 (Sigler and Miller 1963), and reproducing populations of walleye were established by fish stockings in Duchesne River reservoirs (Fig. 1) in the 1960s and 1970s (G. M. Davis, personal communication).

The Green River basin of Colorado and Utah is an important recovery area for four rare and endangered Colorado River fishes (reviewed by Joseph et al. 1977, Carlson and Carlson 1982, U.S. Fish and Wildlife Service 1987). However, over 20 nonnative fishes have been introduced into the basin for sport, forage, food, or by accident (Tyus et al. 1982, Fishes of upper Colorado). Impacts of these introduced fishes on the native fauna are not well understood, but the presence of two large piscivores, northern pike, *Esox lucius*, and walleye, *Stizostedion vitreum*, in areas presently occupied by endangered fishes, is cause for concern. Control of nonnative fishes has been identified as a recovery measure under provisions of an interagency recovery program for endangered fish species in the upper Colorado River basin (U.S. Fish and Wildlife Service 1987). Fish introductions in other locations have eliminated or partially extirpated native fish faunas, and the instability of resultant communities has caused management problems (Moyle et al. 1986).

The purpose of this study was to determine diets of northern pike and walleye in the Green River, and to evaluate the degree of predation on native and endangered fishes. We also document the recent invasion of northern pike into the Green River basin, and the abundance and distribution of northern pike and walleye in the mainstream Green River. The results of this study are interpreted relative

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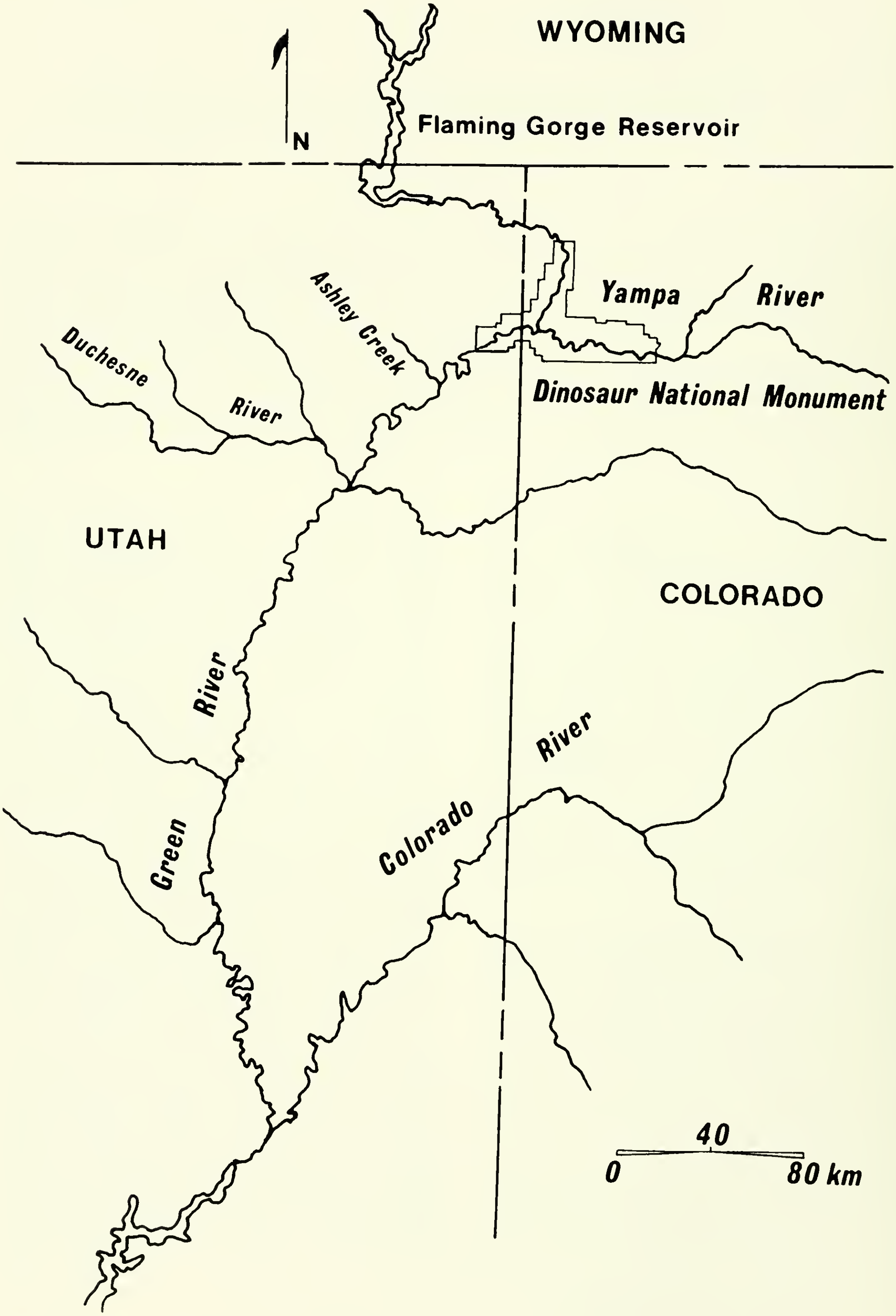
WYOMING
Flaming Gorge Reservoir
N
Yampa River
Ashley Creek
Duchesne River
Dinosaur National Monument
UTAH
COLORADO
Green River
Colorado River
0
40
80 km

Fig. 1. Map of the study area.

to potential interactions of these species with sympatric endangered Colorado River fishes.

METHODS

Northern pike and walleye were primarily collected by electrofishing. Sampling was conducted from April to November 1979–1981 and from April to June 1984–1988 in 517 km of the mainstream Green River. The study area included the mainstream Green River from its confluence with the Yampa River in Dinosaur National Monument to a point 35 km above the confluence of the Green and Colorado rivers (Fig. 1). The lower 73 km of the Yampa River was also sampled 1984–1989. In 1989, spring sampling was conducted in the lower 73 km of the Yampa River and in the Green River in a 208-km reach below its confluence with the Yampa River (Fig. 1).

In 1979–1981, fishes were sampled with a variety of gear, including electrofishing, seines, trammel nets, and wire traps, depending on gear suitability; sampling was conducted during prerunoff, runoff, and post-runoff conditions. In 1984–1988, sampling included only alongshore electrofishing in the prerunoff and early runoff period and involved continuous downstream coverage with a pulsed DC unit. Electrofishing collections in which all shoreline habitats were sampled were considered representative collections, and catches of fishes per hour (C/h) sampled were recorded. Some opportunistic spring electrofishing was also conducted in suspected northern pike and walleye habitats; however, no C/h data were reported for these samples.

All northern pike and walleye collected were measured for total length (TL). Location of capture was also noted. After 1983, all fish were sacrificed and stomach contents identified to the lowest possible taxon with the aid of a 25X binocular dissecting scope. The date, location, and water conditions at the point of capture of all females with ripe eggs and fully developed ovaries were recorded. We also obtained 49 northern pike and 11 walleye stomachs from other workers and identified their contents.

RESULTS

Abundance and Distribution

TABLE 1. Catches of adult northern pike (*Esox lucius*) and walleye (*Stizostedion vitreum*) per hour of electrofishing (C/h), in the Green River, Utah, April–June 1984–1988 (n = number of fish). Upper Green River = km 337.8–552, lower = km 35–337.7.

River location	Hours fished	Northern pike		Walleye	
		n	C/h	n	C/h
		1984			
Upper	101.2	20	.20	15	.15
Lower	32.3	0	—	0	—
		1985			
Upper	886.9	4	.005	8	.01
Lower	28.9	0	—	0	—
		1986			
Upper	753.2	5	.01	17	.02
Lower	35.9	0	—	0	—
		1987			
Upper	760.1	16	.02	8	.01
Lower	37.2	1	.03	1	.03
		1988			
Upper	441.5	9	.02	0	—
Lower	43.0	3	.07	1	.02

Eighty-four northern pike were collected from 1979 to 1989, including 33 females in breeding condition (mature ovaries with ripe eggs). Ripe females were captured in April–June in the mainstream Green River at water temperatures of 10–19 C. All pike were considered adults or large juveniles based on size (average = 619 mm TL, range 321–1,045 mm; Carlander 1969). Average catch of northern pike increased 0.05–0.14 fish per hour from 1984 to 1988 (Table 1). Seventy-eight percent (n = 59) of the pike were collected in the upper Green River in 1984–1988, but many of these (43%) were taken in shallow, low-velocity, shoreline habitats at the mouth of Ashley Creek. Northern pike were spotty in distribution but sometimes abundant in semiimpounded habitats. Their captures were often associated with prominent aquatic and bank vegetation.

We captured two tagged northern pike in this study. These adult fish (594 and 820 mm TL) were tagged by Colorado Division of Wildlife personnel in the Yampa River in 1982 and 1988 (E. J. Wick and T. P. Nesler, personal communication). One fish had moved about 110 km between 15 April 1982 and 10 May 1983 when we recaptured it in the Yampa River at km 18.4. The other pike had

TABLE 2. Contents of 123 northern pike (*Esox lucius*) stomachs taken in the Green River basin, Utah and Colorado, 1984–1989.

Species	Status[a]	Number of prey	Frequency (%)
		FISHES	
unidentified fish	—	40	10.6
Notropis lutrensis	I	24	7.3
Pimephales promelas	I	15	4.1
Catostomus latipinnis	N	6	4.1
Rhinichthys osculus	N	7	3.3
unidentified *Notropis* spp.	I	6	2.4
Gila atraria	I	3	2.4
Catostomus discobolus	N	2	1.6
Ictalurus punctatus	I	2	1.6
Cyprinus carpio	I	3	0.8
Notropis stramineus	I	2	0.8
unidentified Cyprinidae	I	1	0.8
unidentified *Gila* spp.[b]	—	1	0.8
Oncorhynchus mykiss	I	1	0.8
Oncorhynchus clarki	I	1	0.8
Richardsonius balteatus	I	1	0.8
		OTHER	
empty	—	—	54.5
Rana pipiens	N	1	0.8
Lampropeltis spp.	N	1	0.8
detritus	—	—	0.8

[a] N = native species, I = introduced species.
[b] suspected *Gila robusta*

traveled 78 km from 16 June 1988 to 23 May 1989, when it was recaptured at km 4.8. Growth of these fish averaged only 10 mm TL.

Walleye were also captured in the upper Green River (90%, n = 50) and averaged 511 mm TL (range 395–686 mm). These fish were presumed juveniles and adults, based on size (Carlander 1969). More widely dispersed than pike, walleye were usually captured in a variety of slow shoreline runs, usually associated with emergent or bank vegetation. One ripe female walleye (577 mm TL) was captured in the upper Green River on 15 May 1984 at a water temperature of 13 C. We captured one tagged walleye at the mouth of the Duchesne River on 21 May 1984. This fish was tagged by BIO/WEST Incorporated on 13 April 1979 at a point about 37 km upstream in the Green River (L. Crist, personal communication). This fish grew about 62 mm TL in five years.

Foods

Northern pike stomachs (n = 123) were usually empty (54.5%), but of the remainder, 97.6% contained fishes (Table 2). Red shiner, *Notropis lutrensis*, and fathead minnow, *Pimephales promelas*, were most frequently consumed of nine nonnative fishes. Flannelmouth sucker, *Catostomus latipinnis;* bluehead sucker, *C. discobolus;* and speckled dace, *Rhinichthys osculus*, were the native fishes consumed. Other prey items included a leopard frog, *Rana pipiens*, a king snake, *Lampropeltis* spp., and detritus. Thirteen stomachs (10.6%) contained fish remains that could not be identified.

Walleye in the Green River primarily consumed fishes, including 5 nonnative and 1 native species (Table 3). Of 61 stomachs examined, 24 (39.3%) were empty and 10 (16.4%) contained unidentifiable fish remains. Channel catfish, *Ictalurus punctatus*, and fathead minnow were the most frequently consumed nonnative fishes, and flannelmouth sucker was the only native fish consumed. Vascular plant material was found in one walleye stomach.

DISCUSSION

Northern pike, introduced in the Yampa River drainage in 1977, was presumed absent in Green River until first reported in 1981 (Tyus et al. 1982, Fishes of upper Colorado). We captured the fish only in the upper Green River (km 337.8–552) from 1981 to 1986. Pike invaded the midsection (km 192–337.7) by

TABLE 3. Contents of 61 walleye (*Stizostedion vitreum*) stomachs taken in the Green River basin, Utah and Colorado, 1984–1989.

Species	Status[a]	Number of prey	Frequency (%)
		FISHES	
unidentified fish	—	38	16.4
Ictalurus punctatus	I	37	16.4
Pimephales promelas	I	35	9.8
Cyprinus carpio	I	4	6.6
Lepomis cyanellus	I	4	3.3
Catostomus latipinnis	N	1	1.6
unidentified Cyprinidae	I	2	1.6
Ictalurus melas	I	1	1.6
		OTHER	
empty	—	—	39.3
fish eggs	—	—	1.6
vascular plant material	—	—	1.6

[a] N = native species, I = introduced species.

1987, and it was first captured below Green River, Utah (km 192), in 1988. This invasion and downstream movement is supported by both the absence of the fish in the Green River in the early 1970s (Holden and Stalnaker 1975) and a first report of pike in the lower Green in 1988 (M. Moretti, personal communication). Although movements of northern pike in large rivers remain poorly documented, some studies in lakes and small streams have shown that the fish can display high mobility (Miller 1948, Ross and Winter 1981) but may move only short distances at a time (Cook and Bergersen 1988). Our recapture of two northern pike indicated that the fish can move long distances (> 75 km/year) in the Yampa River. Long-distance upstream and downstream movement of radiotagged northern pike has also been reported by T. P. Nesler (personal communication).

The majority of fishes consumed by northern pike in this study were soft-rayed forms (Table 2), as previously noted by others (Beyerle and Williams 1968, Weithman and Anderson 1977, Wolfert and Miller 1978). Channel catfish, the only spiny-rayed fish consumed, was found in two stomachs. We could not positively identify roundtail chub, *Gila robusta*, in northern pike stomachs taken from the Yampa River, but presumably one *Gila* spp. was a roundtail chub. T. P. Nesler (personal communication) reported that roundtail chub were present in northern pike stomachs he examined from the Yampa River. Most of the pike we examined were from the Green River where roundtail chub are rare (Tyus et al. 1982, Fishes of upper Colorado), and this may have resulted in the relative absence of roundtail chub as prey in pike stomachs we examined.

Northern pike may spawn in the mainstream Green River, but if so, recruitment is low. We did not capture small northern pike (< 321 mm TL) in this study, and, to our knowledge, pike reproduction has not been noted by others. However, one 115-mm-TL specimen was seined by HMT and others from a shoreline area of the Green River in Dinosaur National Monument on 8 July 1988. It is not known whether this fish hatched in the Green River or was transported there from another location. Also, we captured several ripe female pike, and it is possible that some of these fish spawned in the Green River. Most ripe female pike (76%) had empty stomachs, suggesting a reduction in feeding activity with increasing water temperatures and ripening ovaries (Frost 1954, Lawler 1965).

Walleye were rare in the Green River, and their long period of residency suggests that their numbers will probably not increase. Walleye were easily captured by electrofishing, and very few fish that we sighted escaped capture. However, it was difficult to capture northern pike with electrofishing, and many fish escaped. A direct comparison of the relative abundance of walleye with that of northern pike could be somewhat misleading, and it is noted that walleye were more rare, and northern pike more abundant, than indicated by electrofishing catch rates. We captured only one female walleye with developed ovaries, and that was in May at a water temperature of 13 C. Walleye in other locations usually spawn at cooler water temperatures (3.3–7.2 C, Sigler and Miller 1963; 5.6–11.1 C, Scott and Crossman 1973). No small walleye (< 395 mm TL) were captured in this study.

Young of the endangered humpback chub, *Gila cypha;* bonytail chub, *G. elegans;* razorback sucker, *Xyrauchen texanus;* and Colorado squawfish, *Ptychocheilus lucius*, may be potential prey for northern pike and walleye. None of these fishes were identified in stomachs of northern pike or walleye, but our ability to detect such predation was constrained by a small sample size of stomachs that contained food, rarity of endangered fishes, and inability to identify all of the fishes eaten.

Sympatry of adults of northern pike, walleye, and endangered fishes is a cause for concern, particularly if resource sharing occurs during periods of limited availability. We collected northern pike, walleye, and Colorado squawfish in similar shoreline habitats in the mainstream Green River; in addition, radiotagged northern pike and Colorado squawfish were syntopic in the Green and Yampa rivers (Valdez and Masslich 1989, Wick and Hawkins 1989). Northern pike were captured in shallow, flooded habitats also utilized by razorback sucker.

Stocking programs for northern pike and walleye have been discontinued by state agencies in Colorado and Utah (G. M. Davis and P. J. Martinez, personal communication), and the relative absence of small fish of both species suggests that reproduction in the mainstream Green River is low or nonexistent during most years. However, the continuing invasion of northern pike and walleye into the Green River from established, reproducing stocks should be monitored, and their interactions with endangered fishes further evaluated until it can be more clearly demonstrated that competition or predation on endangered fishes does not occur or pose a serious threat. The increasing abundance and spread of northern pike, the diversity of fishes consumed, and its syntopy with endangered fishes make this voracious piscivore a potential threat to endangered Colorado River fishes.

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INFLUENCE OF SOIL FROST ON INFILTRATION OF SHRUB COPPICE DUNE AND DUNE INTERSPACE SOILS IN SOUTHEASTERN NEVADA

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ABSTRACT.—The influence of soil frost on the infiltration rate of shrub coppice dune and dune interspace soils was evaluated near Crystal Springs, Nevada, using simulated rainfall. The infiltration rate of the coppice dune soil was greater than the dune interspace soil under frozen or unfrozen conditions. Because of different vegetation cover and surface soil characteristics, coppice dune and dune interspace soils responded differently to freezing, thus imposing a spatial and temporal response to infiltration rate. Infiltration rate of soils with porous concrete frost increased as the soils thawed during simulated rainfall, but soils with nonporous concrete frost allowed very little infiltration to occur. Both coppice dune and dune interspace soils that were classified in January as having granular frost had a higher infiltration rate than the same unfrozen soils in March.

Soil frost influences water infiltration rates and is often a major influence on runoff (Gray and Granger 1987, Harris 1972, Haupt 1967, Kane and Stein 1983, Klock 1972, Kuzick and Bezmenov 1963, Wilcox et al. 1989, and Zuzel and Pikul 1987). Areas where soil frost strongly influences infiltration are characterized by cold winters, transient snow cover, and soils that may freeze and thaw several times each winter, in addition to a diurnal freeze-thaw cycle (Pikul and Allmaras 1986, Zuzel et al. 1986). Infiltration rate of frozen soil is strongly influenced by the structure of the soil frost, which is determined in part by the soil water content at the time of freezing. Concrete frost has been identified as having the greatest impact on infiltration rates (Haupt 1967, Lee and Molnau 1982, Story 1955).

The spatial influence of shrub coppice dune and dune interspace soils on infiltration of unfrozen soil was originally established by Blackburn (1975) and verified by numerous other investigators (Johnson and Gordon 1988, Swanson and Buckhouse 1984, Thurow et al. 1986, Wood and Blackburn 1981, Wood et al. 1987). Because shrub coppice dune and dune interspace soils have different vegetation cover and surface soil characteristics, we hypothesized that they will respond differently to soil freezing and thawing, thus imposing a spatial and temporal response to infiltration during winter. The study objective was to determine the spatial variation in infiltration rates of frozen and unfrozen shrub coppice dune and dune interspace soils.

STUDY AREA

The study area is located in southeastern Nevada about 7 km west of Crystal Springs, 37°20′ N latitude, 115°20′ W longitude at 1,200 m elevation, and 9 km east of the 1,850–2,100 m ridgeline of the Pahranagat Range. The normal annual precipitation of 330 mm occurs mostly during winter as snow or during July and August as thundershowers. Winters are characterized by periodically cold temperatures with frequent diurnal freeze-thaw cycles.

Blackbrush (*Coleogyne ramosissimum*) is the dominant shrub, with 22% crown cover; associated species are joint fir (*Ephedra nevadensis*) and box thorn (*Lycium andersonii*), each with 2% crown cover. Herbaceous cover is sparse. The study site is located on the tops of long, narrow alluvial fans with 5% slope to the east, and the soils are loamy-skeletal, mixed, thermic, shallow, Typic Durorthids.

Two major types of surface soils are found on the study site: the coppice dune soil under shrubs and the barren interspace soil between shrubs. The coppice dune soil covers 35% of the surface, whereas interspace soil covers 65%. The A horizon of the coppice soil is characterized by a weakly subangular blocky structure and a gravelly sandy loam texture. Interspace soils have gravel pavement several pebbles thick over the mineral soil. The 50-mm-thick, loamy, crusted A horizon is massive, has vesicular pores, and is broken into 80–150-mm-diameter polygons. The crusted interspace soil slakes and disperses readily when wetted.

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Methods

Infiltration rates were determined using a drip-type rainfall simulator (Blackburn et al. 1974) with simulated raindrops 2.5 mm in diameter. Drops falling 2.1 m reach 5.25 m sec^{-1} or 71% of the terminal velocity achieved by raindrops in an unlimited fall (Laws 1941). Simulated rainfall was applied on frozen soil in January and on unfrozen soil in March 1974 at a rate of 76 mm hr^{-1} for 30 min. The rainfall intensity was chosen to assure runoff from each study plot. Runoff plots (280 × 500 mm) were randomly placed on 16 and 6 shrub coppice dune soils and 13 and 5 interspace soils during the January and March sample dates, respectively. This sample size is considered adequate for rangeland conditions (Wood 1987). Shrubs were cut at ground level and removed from the coppice dunes to reduce rainfall interception losses.

Volume of runoff was measured every 5 min for 30 min. Infiltration rates were determined as the difference between simulated rainfall and runoff volumes. Soil frost was characterized adjacent to each runoff plot prior to the simulated rainfall event. Three structural forms of soil frost were observed and subjectively classified according to criteria by Hale (1951) and Haupt (1967). Granular frost consisted of scattered granules of ice binding mineral soil together. Nonporous concrete frost was characterized by dense, thin ice lenses and ice crystals. Porous concrete frost was less dense than concrete frost, but frozen chunks of soil were harder to break. Porous concrete frost was further defined by resistance to repeated thrusts of a pick before being punctured. Water used for rainfall simulation averaged 4 C in January and 9 C in March. Analysis of variance and least significant difference mean separation tests (Snedecor and Cochran 1971) were used to test for differences between infiltration rates of the coppice dune and dune interspace soils for the January and March sample dates.

Results and Discussion

All plots during January were classified as having soil frost 100 mm thick located about 50 mm below the surface. Three of the coppice dune and five of the interspace plots were classified as granular frost. The remaining plots of both soils were characterized as porous or nonporous concrete frost, of which 12 coppice dune and 6 interspace plots were classified as porous concrete frost.

Infiltration rate after 25 min was significantly greater for coppice dunes than for dune interspaces under both frozen and unfrozen soil conditions (Fig. 1, Table 1). Similar relationships between unfrozen shrub coppice dune and dune interspace soils have been reported by Blackburn (1975), Johnson and Gordon (1988), Thurow et al. (1986), and Wood and Blackburn (1981). The differences in infiltration of coppice dune and dune interspace soils have been attributed to differences in vegetation and surface soil characteristics (Blackburn 1975, Johnson and Gordon 1988). Infiltration of unfrozen rangeland soil is usually characterized by a high initial rate that decreases rapidly with time and stabilizes at some constant rate within 30 to 60 min (Fig. 1). However, mean infiltration rates in January declined within the first 15 min for the coppice dune soils and within 20 min for interspace soils; in neither case did they stabilize at a constant rate. Infiltration rates for both soils increased during the latter part of the rainfall due to thawing of the porous concrete soil frost layer of some plots (Figs. 2, 3). As a result, there was no significant difference in 30-min infiltration rates between frozen and unfrozen dune interspace soils. However, 30-min infiltration rates tended to be lower in the frozen coppice dune soils in January than in unfrozen soils in March (Fig. 1).

Infiltration rates of coppice dune plots classified as granular frost were similar to the rainfall application rate and 10 mm hr^{-1} greater than when the soils were unfrozen in March (Figs. 1, 2). Coppice dune plots classified as porous concrete frost and thawing during the rainfall event reached a minimum

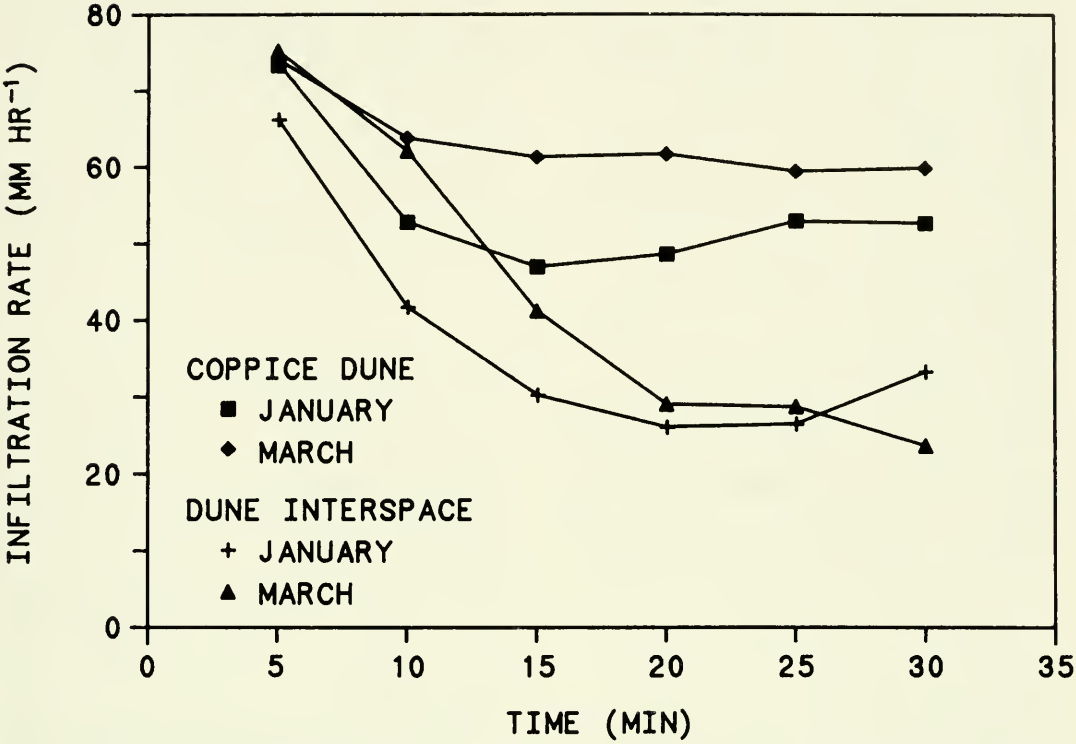

Fig. 1. Mean infiltration rates for all coppice dune and dune interspace soils in January and March, Crystal Springs, Nevada.

TABLE 1.—Significant difference of five-minute interval infiltration rates for coppice dune and dune interspace soils for the January and March sample dates[1], Crystal Springs, Nevada.

Soil/Sample date	Time (minutes)					
	5	10	15	20	25	30
Coppice March vs. coppice January	ns[2]	ns	ns	ns	ns	ns
Coppice March vs. interspace March	ns	ns	ns	*	*	**
Coppice March vs. interspace January	ns	ns	**	**	**	*
Coppice January vs. interspace March	ns	ns	ns	ns	*	**
Coppice January vs. interspace January	ns	ns	ns	**	**	*
Interspace January vs. interspace March	ns	ns	ns	ns	ns	ns

[1] Sample size: coppice, January n = 16, March n = 6; interspace, January n = 13, March n = 5.

[2] Level of significance (P ≤ .01 = **; P ≤ .05 = *; ns = nonsignificant at P > .05) determined with a one-way analysis of variance and a least significant difference (lsd) mean separation test.

infiltration rate after 20 min of 44 mm hr^{-1}, but 30-min rates increased to a rate similar to that of the granular frost plots (Fig. 2). The one porous concrete frost plot that remained frozen during the rainfall event reached a minimum rate after 15 min and then increased slightly during the remainder of the event to 33 mm hr^{-1}.

Infiltration rate at 30 min of interspace soil with granular frost was 14 mm hr^{-1} greater than when the soil was unfrozen in March. Interspace plots that were initially classified as porous concrete frost and thawing during the rainfall event reached a minimum infiltration rate of 12 mm hr^{-1} after 20 min, after which rates increased and were similar to unfrozen soils in March. Infiltration rate of the interspace nonporous concrete frost plot decreased to 2 mm hr^{-1} at 30 min, 21 mm hr^{-1} lower than the 30-min rate of unfrozen soils in March. Other researchers have reported similar infiltration response caused by soil frost

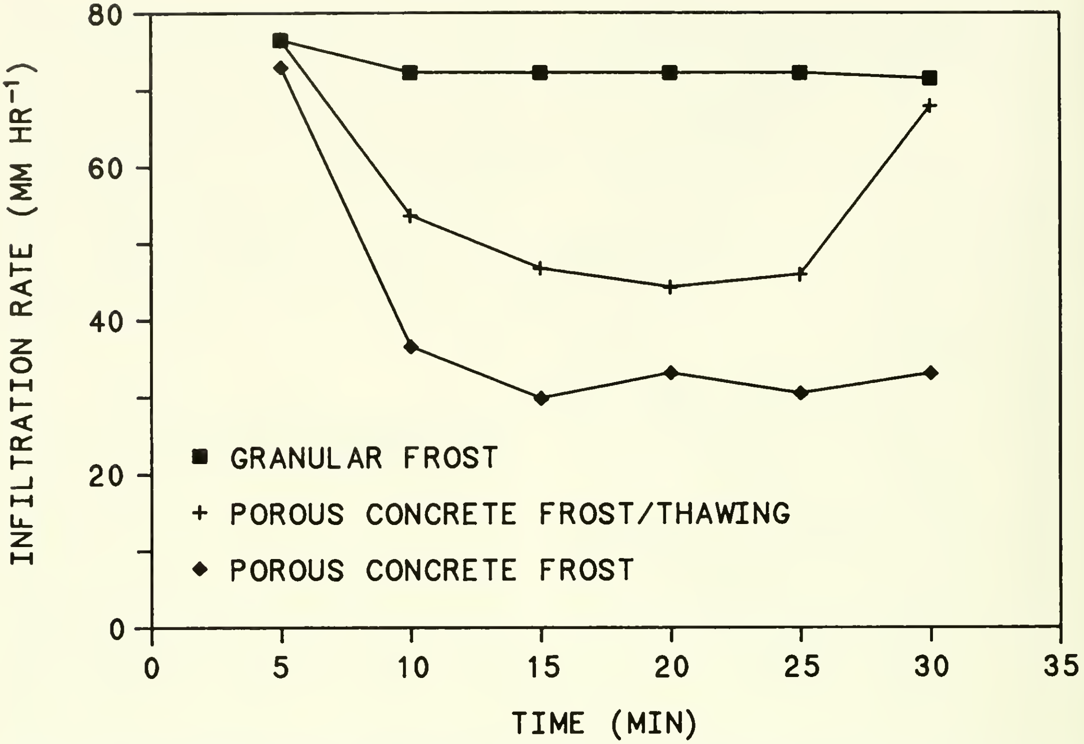

Fig. 2. Infiltration rates in January for coppice dune soils classified as having granular frost, porous concrete frost that was thawing during the rainfall event, and porous concrete frost, Crystal Springs, Nevada.

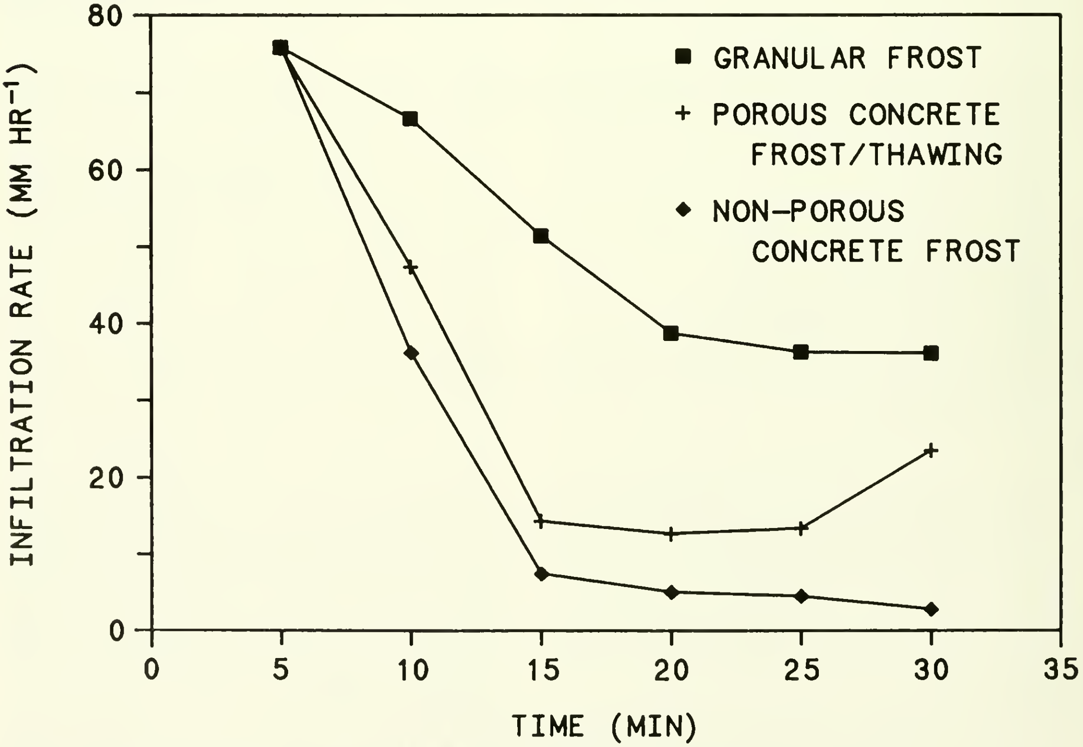

Fig. 3. Infiltration rates in January for dune interspace soils classified as having granular frost, porous concrete frost that was thawing during the rainfall event, and nonporous concrete frost, Crystal Springs, Nevada.

structure. Trimble et al. (1958), in New Hampshire, reported infiltration rate of soils with granular frost to be higher than that of unfrozen soils. Haupt (1967) found, for the eastern slope of the Sierra Nevada, the infiltration rate of porous concrete frost to increase as the soil thawed. Trimble et al. (1958) and Stoeckeler and Weitzman (1960) found infiltration rates of nonporous concrete frost in northern Minnesota to be very low.

CONCLUSIONS

The infiltration rate of shrub coppice dune soils was greater than dune interspace soils under frozen and unfrozen conditions. Concrete frost located 50 mm below the surface had a pronounced effect on infiltration rates. Infiltration rates of soils with porous concrete frost increased as the soils thawed during the simulated rainfall, but soils with nonporous concrete frost allowed very little infiltration to occur. Both coppice dune and dune interspace soils classified as having granular frost had a higher infiltration rate than the same unfrozen soils in March. Due to different vegetation cover and surface soil characteristics, shrub coppice dune and dune interspace soils responded differently to soil freezing and thus imposed a spatial and temporal response to infiltration rate.

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SEED PRODUCTION AND SEEDLING ESTABLISHMENT OF A SOUTHWEST RIPARIAN TREE, ARIZONA WALNUT (*JUGLANS MAJOR*)

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ABSTRACT.—A four-year study of five populations has revealed influences on seed production and seedling establishment of the Southwest riparian tree *Juglans major*. Germination is abundant after production of large seed crops (masts), but masts are produced infrequently. Within years, germination is stimulated by summer rains, enabling seedlings to establish on riparian terraces as well as streambanks. Traits such as capacity for dormancy during summer drought allow some seedlings to survive on terraces, but abundant rainfall is essential for high rates of seedling success. Ranges of moisture tolerance vary among seeds collected from different populations, suggesting that ecotypes may exist between riparian sites with dissimilar moisture regimes. Population-based differences are associated, in part, with differences in seed size.

Arizona walnut (*Juglans major* [Torr.] Heller) is a member of the "Interior riparian deciduous forest," an assemblage of trees that grow along streams in the Interior Southwest (Brown 1982). Walnut sometimes dominates this community (Szaro 1989), but more often it occurs at relatively low densities and frequencies. This distribution pattern, while indicating that establishment occurs infrequently, does not reveal the stage where regeneration is limited. Sudworth (1934) suggested low rates of seed production and high rates of seed predation by tree squirrels as possible natural causes of infrequent establishment; seedling mortality from cattle grazing also may play a role (Rucks 1984).

Lack of suitable germination and establishment sites may limit recruitment, but little is known regarding the relationship between these requirements and *J. major*. Certain generalizations have been made about the distribution of walnut trees, but the habitat characteristics of trees may differ from those in which the seedlings established. A study that specifically addressed riparian seedlings revealed that seedlings of *J. major*, a facultative riparian species, establish in many microsites throughout the riparian zone. This is in contrast to seedlings of obligate riparian trees such as Arizona alder (*Alnus oblongifolia* Torr.) that occur only immediately adjacent to the stream (Larkin 1987). Larkin conducted her study, however, in a wet, montane area of central Arizona; germination "safe sites" for walnut may be more restricted in drier riparian sites such as along ephemeral streams. For example, seed burial may become a prerequisite of germination as soil moisture decreases, as is true for certain oaks (Barrett 1931).

Germination and establishment of walnut or other riparian species may also vary as a function of genetic differences between populations. The existence of riparian ecotypes is not a new idea (e.g., Hook and Stubbs 1967), and riparian populations may differ between isolated Southwest watersheds with different hydrologic characteristics. Other studies in this series on walnut reproduction have identified differences between populations in floral ratios and seed weight (Stromberg 1988), indicating that *J. major* shows either plastic responses or genetically based responses to environmental differences within and between riparian sites. The objectives of this study were to: (1) identify factors that limit seed production and seedling recruitment of *J. major* between sites and between years; (2) determine how germination requirements vary between microsites; and (3) determine how seedling growth response to soil moisture differs between populations.

METHODS

Seed production, germination, and seedling survival of *J. major* were studied through field and greenhouse experiments and field observations. Five sites were selected in central Arizona: Hitt Wash, an ephemeral stream near Prescott National Forest; Rock Creek, an intermittent stream in the Mazatzal Mountains; and perennial streams (South Fork Walnut Creek in Prescott National Forest and two sites along Workman Creek in the Sierra Ancha Mountains) (Stromberg 1988). Elevations vary from 1,100 m at Rock Creek to 2,100 m at Aztec Peak.

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Field Observations

Twenty trees were selected at each site, and samples of 20 shoots per tree were selected for monitoring of seed production from 1983 to 1986. Average values per tree were calculated for seed production per shoot and for flower production, flower abortion, seed weight, and seed viability (Stromberg 1988). A mast (large seed crop) is operationally defined in this study as a crop 33% larger than average for the study.

Demography of natural seedlings was studied to determine when, where, and how many seeds germinate, and to compare survival rates between microsites. One walnut tree near the stream and one on the adjacent terrace with nearby seedlings were selected at each site. Each marked the center of an 8-m-radius circular plot. All seedlings in the plots were tagged and scored monthly from May to October of 1983, 1984, and 1985 for stem height, leaf length and number, and mortality. Twenty seedlings in a plot at Hitt Wash were excavated to measure depth of the nut in the soil profile.

Field Experiments

Seeds were sown in field exclosures in fall 1982 and 1983 to test for influence of microsite (soil moisture and canopy cover) and burial depth on germination and survival. Exclosures protected seedlings from trampling and predation. Four microsites (streamside, open canopy; terrace, open canopy; streamside, closed canopy; terrace, closed canopy) were selected per site, with three replicate exclosures per microsite. Exclosures were constructed from 1.3-cm hardware cloth, and were 0.6 × 0.6 × 1 m high, with 15 cm of mesh below ground. Seeds were planted 36 per exclosure in 6 rows in 3 planting treatments: surface sown, partially buried, or buried 2 cm deep. Sites were planted with their own seeds (except for Workman Creek and Rock Creek), and seedling size and survival were recorded through 1985. Microsite soil moisture was recorded monthly with a dew-point psychrometer, and canopy cover was estimated visually (Stromberg 1988). Influences on germination and seedling survival were analyzed through multiple regression analysis of germination and survival percentages with average seasonal values for microsite moisture level, canopy cover, and herbaceous cover.

Greenhouse Experiments

Nuts were collected in 1983 from trees at Rock Creek, Hitt Wash, and Walnut Creek to test for influence of seed weight and seed source on germination and seedling growth. Nuts were sown in the greenhouse in loam soil in polyethylene-lined pots under four watering regimes. One regime was watered every other day to maintain saturated conditions. Others were watered at less-frequent intervals, producing average soil moisture contents by dry weight of 80%, 40%, and 20%. Seeds were sown on the surface and buried 2 cm deep. Seven nuts from each of 24 parent trees were sown per treatment. Germination percent and speed and seedling survival were monitored. Eight weeks after emergence, plants were harvested for measurement of dry weight, stem height, and root length. At each soil moisture level, regression analysis was used to test for influence of seed weight, a continuous variable. Duncan's multiple range test was used to test for effects of seed source on germination and seedling growth rates.

RESULTS

Seed Production

Seed production differed substantially between sites and years. All sites had large annual variation in seed production, with annual coefficients of variation ranging from 100 to 140 among sites. Masts were produced in one or two of the four years among sites (Fig. 1). Large crops of seeds, irrespective of viability, were produced more frequently. Some exceptional trees produced four consecutive, large seed crops. Number of large flower crops also varied substantially between sites, ranging from one at Walnut Creek to three at Hitt Wash.

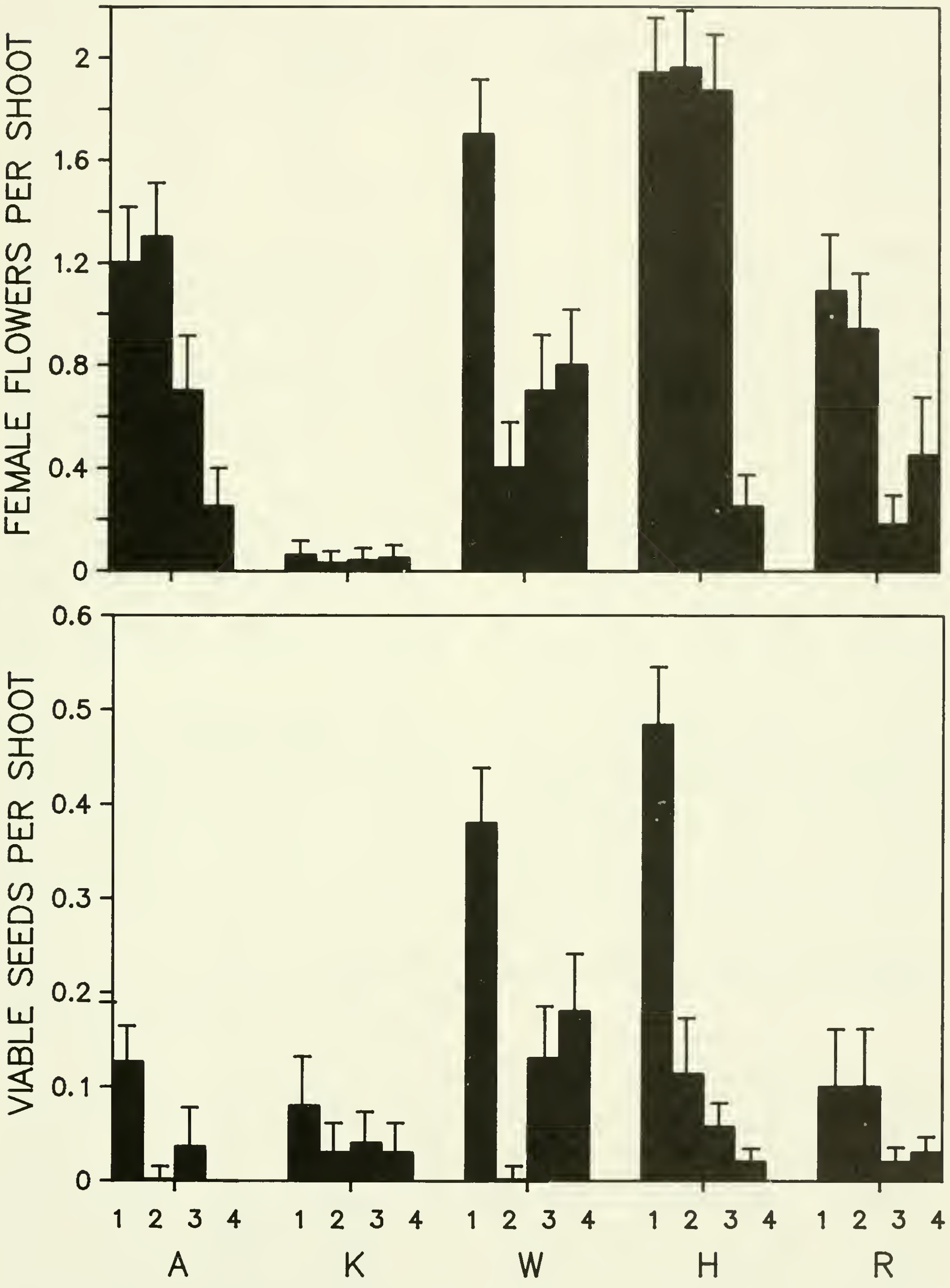

Fig. 1. Site means for female flowers and viable nuts produced per shoot for *Juglans major* from 1983 through 1986 at Aztec Peak (A), Workman Creek (K), Walnut Creek (W), Hitt Wash (H), and Rock Creek (R).

TABLE 1. Average rates of seed production (expressed as viable seeds produced per 100 shoots) and abundance of *Juglans major* seedlings per 200 m^2 at five sites in Arizona.

	Seeds 1983	Seedlings 1984	Seeds 1984	Seedlings 1985	Seeds 1985	Seedlings 1986
Aztec Peak	11	0	0	0	2	0
Workman Creek	9	2	3	1	3	0
Walnut Creek	38	52	0	0	14	23
Hitt Wash	46	207	10	48	6	24
Rock Creek	10	3	10	1	2	1

Masts were produced at all sites in 1983, with abundant viable nuts maturing on trees (Fig. 1). Seed production patterns in following years differed among sites. Seed crops were low in different years among sites, and crops failed at different reproductive stages. The most common causes of crop failure were reductions in numbers of female flowers and production of inviable, low-weight seeds; high rates of abortion were a less frequent cause. At Walnut Creek, for example, viable nut production was lowest in 1984, a result of few flowers and inviable seeds (3% viable). Hitt Wash trees produced a large crop of viable seeds only in 1983; seed production was limited at sequentially earlier reproductive stages from 1984 to 1986. In 1984 many flowers were produced and matured, but seed viabilities were low (28% viable). In 1985 flowers were again abundant, but many (96%) were aborted. In 1986 Hitt Wash finally had a sharp decline in female flowering, resulting in a low crop size. Rock Creek trees showed a third pattern. Following the mast of 1983, moderate numbers of flowers and viable seeds were produced in 1984. This was followed by large declines in flower number in 1985. Moderate numbers of viable seeds were produced in 1986.

Field Germination

Natural seedling abundance differed substantially between sites and years. These differences were related, in part, to seed production rates. Seedlings were abundant only at sites that produced many seeds (Hitt Wash and Walnut Creek) (Table 1). Few seedlings were present at Rock Creek, despite moderate seed production, because of seed predation by Arizona gray squirrels (*Sciurus arizonensis;* see Stromberg 1988). Annual seedling abundance was influenced by size of the prior year's crop of viable seeds, since seeds generally germinated the year after they were produced. The mast year of 1983 was followed by abundant seedlings in 1984, whereas the largely inviable seeds produced during dry 1984 resulted in low or no recruitment in 1985. Rainfall in the year of germination may also have increased seedling numbers. This is suggested by the greater abundance of seedlings in wet 1983 than in dry 1984 (e.g., 132 vs. 52 at Walnut Creek), despite production of masts in 1982 and 1983. Within years, seeds germinated during wet seasons (Table 2). Most germinated during the late summer (August–September) rains. Seeds germinated infrequently in May and only during wet springs or in wet streambank microsites; none germinated during the July dry period.

Germination increased with microsite soil moisture, although moisture did not exclusively regulate germination ($r^2 = .24$, df = 14, $P < .04$; values for exclosures). Few seeds germinated on open terraces, particularly at the low-elevation sites (Rock Creek, Hitt Wash) (Table 3) where soils were drier (Table 4). Canopy cover was positively associated with germination percentages within these drier microsites, and dense herbaceous cover was negatively associated with germination rates. Together, soil moisture, canopy cover, and herbaceous cover explained 45% of the variation in germination percentages between microsites.

Few surface-sown nuts germinated in any microsite (Table 3). Burial increased germination rates within all microsites at all sites except Workman Creek, where burial in saturated soil decreased germination. Partially buried seeds germinated in moderate numbers in streambanks and under canopy; complete burial was necessary for germination in open terraces. Lack of burial limited germination of natural seed populations. For example, many seeds were ungerminated on the soil surface at Hitt Wash terrace. Excavation of

TABLE 2. *Juglans major* seedling recruitment by month (May through October) in streamside and terrace plots at sites in Arizona. Plots are 200 m^2.

		1983						1984						1985					
Site	Plots	M	J	J	A	S	O	M	J	J	A	S	O	M	J	J	A	S	O
Workman	Terrace	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Creek	Streamside	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Walnut	Terrace	0	0	0	53	41	0	0	0	0	18	12	0	0	0	0	0	0	0
Creek	Streamside	0	0	0	22	13	0	0	0	0	14	8	0	0	0	0	0	0	0
Hitt Wash	Terrace	6	3	0	92	43	2	0	0	0	105	48	1	0	0	0	21	7	0
	Streamside	14	5	0	35	13	0	0	0	0	47	25	1	2	0	0	13	5	0
Rock Creek	Terrace	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Streamside	0	0	0	3	0	0	0	0	0	1	0	0	0	0	0	1	0	0

TABLE 3. Germination percentages of *Juglans major* sown at three planting depths in four microsites. Average seed viability was 60%. Values are means and standard deviations for 3 groups of 12 nuts. Planting depths are: buried at 2 cm, partially buried, and surface sown. Sites are: Aztec Peak (A), Workman Creek (K), Walnut Creek (W), Hitt Wash (H), and Rock Creek (R). NA = not available.

	Streambank, canopy			Streambank, open		
Site	Buried	Partially buried	Surface	Buried	Partially buried	Surface
A	0 [0]	0 [0]	0 [0]	0 [0]	0 [0]	0 [0]
K	4 [6]	25 [0]	8 [0]	NA	NA	NA
W	NA	NA	NA	29 [6]	13 [6]	8 [0]
H	45 [30]	3 [5]	0 [0]	46 [6]	0 [0]	0 [0]
R	50 [18]	5 [5]	0 [0]	50 [15]	0 [0]	0 [0]

	Terrace, canopy			Terrace, open		
Site	Buried	Partially buried	Surface	Buried	Partially buried	Surface
A	0 [0]	0 [0]	0 [0]	0 [0]	0 [0]	0 [0]
K	21 [6]	25 [0]	8 [0]	50 [33]	0 [0]	0 [0]
W	35 [19]	16 [11]	3 [5]	28 [16]	0 [0]	0 [0]
H	53 [5]	25 [14]	8 [9]	0 [0]	0 [0]	0 [0]
R	21 [12]	0 [0]	0 [0]	4 [8]	0 [0]	0 [0]

TABLE 4. Soil water potential at 30 cm (−MPa) for terrace (T) and streamside (S) open canopy microsites during May, July, and September of 1983, 1984, and 1985. Sites are: Aztec Peak (A), Workman Creek (K), Walnut Creek (W), Hitt Wash (H), and Rock Creek (R).

		1983			1984			1985				
Site	Microsite	May	Jul	Sep	May	Jul	Sep	May	Jul	Sep	Mean	[± SD]
A	T	0.02	0.15	0.01	0.68	0.83	0.06	0.11	0.79	0.06	0.30	[0.33]
	S	0.01	0.16	0.00	0.54	0.63	0.03	0.06	0.54	0.03	0.22	[0.25]
K	T	0.03	0.19	0.01	1.03	1.36	0.06	0.24	1.16	0.06	0.46	[0.52]
	S	0.01	0.17	0.00	0.78	0.96	0.02	0.12	0.93	0.04	0.34	[0.40]
W	T	0.03	0.24	0.02	1.18	1.26	0.05	0.42	1.33	0.04	0.51	[0.54]
	S	0.02	0.18	0.00	0.84	0.96	0.02	0.18	1.02	0.02	0.36	[0.42]
H	T	0.03	0.32	0.01	1.65	1.84	0.15	0.48	1.80	0.12	0.71	[0.76]
	S	0.03	0.22	0.02	1.45	1.63	0.05	0.26	1.58	0.06	0.59	[0.69]
R	T	0.04	0.43	0.20	1.86	2.04	0.13	0.64	1.83	0.14	0.81	[0.80]
	S	0.03	0.32	0.02	1.45	1.63	0.05	0.26	1.58	0.06	0.60	[0.68]
Mean		0.03	0.26	0.04	1.27	1.44	0.07	0.32	1.39	0.07		
± SD		0.01	0.09	0.06	0.38	0.39	0.04	0.16	0.35	0.04		

TABLE 5. Germination percentages for *Juglans major* buried in soil or sown on the surface at three soil water contents (by weight) in the greenhouse. No seeds germinated at 20% soil moisture. Seeds are from streambanks (S) or terraces (T) from Walnut Creek (W), Hitt Wash (H), or Rock Creek (R). Values are means and standard deviations.

		Saturated		80% moisture		40% moisture	
Seed source		Buried	Surface	Buried	Surface	Buried	Surface
W	S	21 [21]	50 [7]	50 [7]	0 [0]	7 [7]	0 [0]
	T	0 [0]	50 [29]	42 [18]	0 [0]	21 [21]	0 [0]
H	S	5 [6]	28 [31]	63 [29]	0 [0]	24 [33]	0 [0]
	T	0 [0]	18 [12]	61 [16]	0 [0]	19 [27]	0 [0]
R	S	0 [0]	22 [9]	39 [11]	0 [0]	13 [0]	0 [0]
	T	0 [0]	14 [7]	48 [15]	0 [0]	16 [5]	0 [0]

seedlings revealed that only 5% of the seedlings were from surface nuts, whereas 75% were from partially buried nuts and 20% were buried at depths of 9 to 15 cm in pocket gopher (*Thomomys* spp.) caches.

Greenhouse Germination

Juglans major germinated abundantly in soil with a moisture content of 80–100% by weight (Table 5). Few seeds germinated in the dry soil or saturated soil. Planting depth influenced germination at all soil moisture contents. In the saturated soil, surface-sown seeds germinated in substantially higher percentages than buried seeds. In contrast, seeds required burial for germination at all other moisture contents.

Germination rates in saturated soil varied between populations and with seed weight. Seeds collected from trees along the banks of perennial Walnut Creek germinated in higher percentages than seeds from sites with ephemeral (Hitt Wash) or intermittent (Rock Creek) stream flow (Table 5). Many cohorts from these latter sites did not germinate in saturated soil. Germination percentage in saturated soil also tended to increase as seed weight (g) per cohort decreased ($y = 31.8 - 5.3x$, $r^2 = .15$, df = 22, $P < .05$). Seed weight was not related to germination in dry or moist soil.

Speed of germination varied with soil moisture level and with seed weight. Seeds in moist soil (80–100%) germinated rapidly (16 ± 10 days), whereas seeds in drier soil (40% by weight) germinated 28 ± 12 days after planting. Although variance in germination speed was high within a cohort, median germination speed increased significantly with seed weight for a cohort ($y = -0.5 + 5.5x$, $r^2 = .34$, df = 22, $P < .01$, in 80% moisture). For example, seeds weighing 3 g germinated in 16 days, compared with 38 days for those weighing 7 g.

Seedling Survival in the Field

Seedling mortality had a major role in limiting regeneration of *J. major*. Only 1 of 374 natural 1983 seedlings among the study sites was alive as of fall 1985. Mortality was high in the year of germination and in the two years following (Fig. 2). Most seedlings died in June, typically a dry month, or in winter. Precipitation was sparse in early 1984 (Table 6), and seedlings that germinated in 1983 had high winter mortality: only 7% of Hitt Wash and 9% of Walnut Creek 1983 natural fall cohorts survived until spring 1984. Many that did survive remained dormant through the spring and summer drought of 1984, withholding leaf-out until the late summer rains. In contrast, more than 20% of 1984 cohorts at both sites survived to spring of 1985.

Seedling survivorship varied between microsites (Table 7) as well as between years. A large part of the variation between microsites was attributable to soil moisture. Survivorship after two years increased with soil moisture between exclosures ($r^2 = .31$, df = 14, $P < .05$), with seedlings on open streambanks having highest survival. Seedlings that did survive in dry microsites had high mortality of buds and shoots during their first and second winters, and grew slowly. On terraces, 42% of year-old survivors originated new spring growth from basal buds, 49% from lateral buds, and only 9% from the terminal bud. On streambanks, in contrast, 15% regrew from basal buds, 58% from lateral, and 31% from terminal buds. Second-year seedlings on the open terrace that regenerated from a basal bud had average stem height of 2.5 cm, with

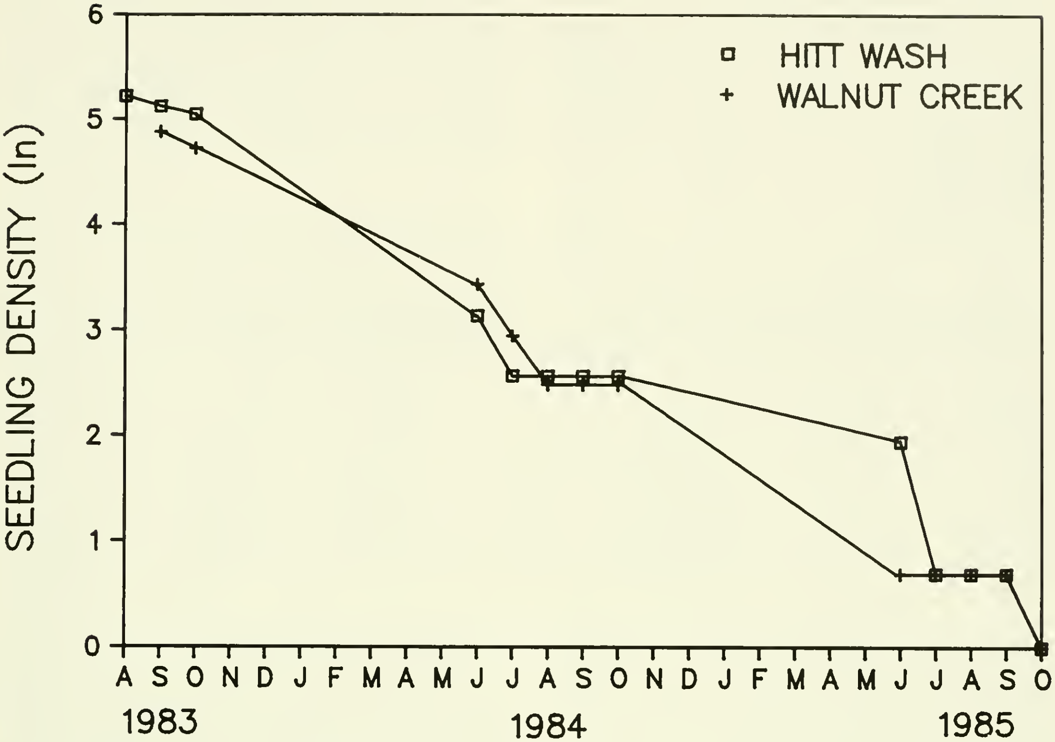

Fig. 2. Seedling survivorship for *Juglans major* that germinated in fall 1983 at Hitt Wash (HW) and Walnut Creek (WC). Values are $\log_e$ of seedlings remaining each month.

TABLE 6. Precipitation (cm) from 1982 to 1986 at a climatic station near the Walnut Creek study site. Average annual precipitation is 39 cm.

	1982	1983	1984	1985	1986
January–June	21	22	3	14	16
July–December	19	31	37	31	30
Total	40	53	40	44	46

as few as two leaves 1 cm long. These seedlings did not markedly increase in size from 1983 to 1985. Seedlings in moist, open areas grew rapidly, as evidenced by a two-year streambank seedling in full sun that reached 44 cm tall.

Flooding killed some streambank seedlings but did not impact terrace seedlings. Fall floods killed 10% of Walnut Creek and 5% of Hitt Wash 1983 streambank seedlings; mortality rates from winter/spring floods were not quantified. Physical impacts of floods included stem breakage, coverage with debris, and scouring of seedlings. Several seedlings resprouted after stem topping.

Herbivory damage from insects also contributed to seedling mortality. Interestingly, seedlings did not have greatest herbivory at sites where adult herbivory was high (see Renaud 1986). Rather, seedlings in specific microsites had greatest leaf loss from herbivores. Seedlings on terraces, under canopy, had greatest herbivory damage; leaf area consumed by October 1983 was 33% ± 15, compared to < 9% for all other microsites.

Effects of cattle grazing were included in the study out of necessity because of the almost ubiquitous presence of cattle in Southwest riparian areas. Two sites, Hitt Wash and Walnut Creek, had heavy to moderate cattle grazing. Seedlings in exclosures at both sites had substantially higher survival rates than those in similar unprotected areas; however, this was also true for the ungrazed sites (Table 7). Adverse impacts of cattle on seedlings included trampling and grazing. At Hitt Wash, 22% of 213 natural seedlings had broken or eaten stems, as did 13% of 130 seedlings at Walnut Creek. Ability of seedlings to recover from trampling and grazing varied between sites; 40% of all stem-damaged seedlings at

TABLE 7. Survival percentages one, two, and four years after germination for *Juglans major* seedlings in exclosures and natural areas in four microsites.

	Exclosures			Natural areas		
Microsite	1 yr	2 yr	4 yr	1 yr	2 yr	4 yr
Stream, open	51	28	16	0	0	0
Stream, canopy	22	15	0	7	0	0
Terrace, open	6	0	0	5	0	0
Terrace, canopy	14	0	0	3	0	0

TABLE 8. Dry weight, root length, shoot height, root:shoot weight ratio, and mortality of eight-week *Juglans major* seedlings in the greenhouse in soil at three moisture contents. Asterisk (*) indicates significant difference between Hitt Wash (H) and Walnut Creek (W). Values are means and standard deviations.

Moisture treatment	Seed source	Dry weight (g)	Root (cm)	Shoot (cm)	R:S ratio	Mortality (%)
40%	H	0.35 [0.05]	25 [2]	9 [2]	1.4 [0.3]	0 [0]
	W	0.44 [0.05]	29 [3]	11 [2]	1.1 [0.3]	0 [0]
80%	H	0.83 [0.14]	34 [7]	16 [2]	0.9 [0.2]	0 [0]
	W	0.76 [0.12]	34 [6]	15 [2]	0.9 [0.2]	0 [0]
Saturated	H	0.12 [0.02]*	4 [2]*	7 [2]*	0.4 [0.1]*	80 [22]*
	W	0.27 [0.04]	13 [3]	10 [3]	0.7 [0.2]	13 [6]

Hitt Wash regenerated a new stem during the same year of breakage, whereas none did so at Walnut Creek.

Greenhouse Seedling Survival

All seedling cohorts had greatest growth in intermediate soil moistures and poorest in saturated soil (Table 8). Root growth in particular was low in saturated soil, and root-to-shoot ratios were low compared to drier soils. Some cohorts, however, grew better than others in saturated soil. Similar to results for germination rates, seedling growth and survival in saturated soil were related to seed weight and seed source. Size and weight of seedlings in saturated soil increased significantly with decreasing seed weight among cohorts (e.g., seed weight in g = 26.5 − 4.5 * root length in cm, $r^2 = .49$, df = 11, $P < .01$). With regard to seed source, cohorts from the perennially saturated streambanks of Walnut Creek had greater root development and survivorship in saturated soil than did cohorts from drier Hitt Wash.

DISCUSSION

Although a survey of five populations is not representative of a species as a whole, this study has highlighted factors influencing recruitment of *J. major*. Low and fluctuating availability of seeds plays a large role in limiting abundance of seedlings between years and sites. The extent of fluctuation in annual seed production by *J. major* is similar to values for other mast-cropping trees (Silvertown 1980), and frequency of mast production is similar to other Juglandaceae (Nixon et al. 1980, Sork 1983, Waller 1979). Seedlings were abundant only after mast years, substantiating the view that infrequent production of viable crops limits regeneration (Sudworth 1934). Rainfall, which varies considerably between years in the Southwest, appears to have an important influence on mast production. The evidence for this, although based on a limited number of years of observation, comes from associations detected between rainfall and the reproductive stages that are critical to production of successful masts—flower production, associated with abundant prior and present year rainfall, and seed weight, which increases with abundant spring rainfall (Stromberg 1988). Seed number between sites is limited variously by low soil moisture and high predispersal seed predation (e.g., Rock Creek) and insect herbivory (e.g., Workman Creek) (Stromberg 1988).

Low rates of germination also limit recruitment to some degree. Whereas moisture for germination and establishment of some obligate riparian trees is provided by stream flow (Fenner et al. 1985), these processes in *J. major*, and perhaps other facultative riparian trees, are influenced in large part by rainfall. Recent documentation of fairly high regeneration rates for walnut in the Southwest (Larkin 1987, Medina 1986) may be a result of long-term moisture cycles, Arizona being in an above-average cycle at the time of these studies.

Although moist areas provided optimum safe sites for germination and seedling establishment, some *J. major* seedlings established on terraces and along ephemeral streams. Seedlings were somewhat drought-tolerant, as indicated by high survival in greenhouse drought conditions, high root:shoot ratios in drier conditions, and ability to survive summer drought via dormancy. Nevertheless, seedling numbers in drier riparian sites were low. Recruitment may be abundant only after a sequence of several wet years—two for production of a large viable seed crop, another for abundant germination, and one or two more for high survivorship. The low frequency of such a sequence may explain the uniform age structure of adult walnut populations at some low-elevation sites (Stromberg 1988).

An additional factor that may limit establishment of seedlings in dry sites is lack of burial. Processes that bury seeds include deposition of flood debris (rare on terraces), caching by pocket gophers (rare except in sandy soils), trampling by large animals, and possibly caching by squirrels. Although tree squirrels commonly cache walnuts (Stapanian and Smith 1978), there is conflicting evidence about the frequency at which they cache nuts of *J. major*. In parts of their range where winters are mild, squirrels immediately consume gathered nuts (Brown 1984). This behavior may contribute to the decline in abundance of walnut at low elevations.

This study suggests that germination and establishment requirements of *J. major* differ between populations, as well as between microsites. Specifically, populations from perennial stream sites appear to be more tolerant of saturated soil at the seed and seedling stages; this should be verified on a larger sample of populations. The greater germination and seedling survival in saturated soil for seeds from such sites may be a consequence of lower oxygen demands of their smaller seeds (Stromberg 1988) or of physiological adaptations (Hook and Crawford 1978). Tolerance of moisture level is known to vary among seeds and seedlings as a result of ecotypic differentiation in morphology or physiology (Hook and Stubbs 1967), and differences in tolerance of flooding and saturated soil are common among trees that grow on sites with different flooding histories (McGee et al. 1981). Isolation of Southwest riparian populations within "mountain islands" with distinct moisture regimes may have led to development of physiological and morphological ecotypes (Little 1950, Thornber 1915).

Whereas small seed size and tolerance of saturated soil are associated with wet riparian sites, the large seeds produced by walnuts on drier sites (Stromberg 1988) may increase survival of seedlings stressed by factors such as drought or grazing. Although purely speculative, the greater ability of Hitt Wash seedlings to recover from trampling and grazing compared with Walnut Creek seedlings may have been a consequence of larger seed size. Large seeds have large cotyledons that remain attached to seedlings for up to a year after germination (Stromberg 1988), allowing young seedlings to regenerate stems (Wetzstein et al. 1983). In any case, differences in seedling responses between walnut populations highlight the need for study of many populations to thoroughly understand reproductive dynamics of any riparian species.

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FORAGE QUALITY OF RILLSCALE (*ATRIPLEX SUCKLEYI*) GROWN ON AMENDED BENTONITE MINE SPOIL

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ABSTRACT.—At peak standing crop, rillscale (*Atriplex suckleyi*) foliage grown on amended bentonite mine spoil contained adequate digestible energy, crude protein, and all mineral elements except phosphorus necessary for cattle, sheep, antelope, and deer. Amendments (sawdust, NPK, gypsum) generally did not affect forage quality. Iron, manganese, aluminum, sodium, and potassium concentrations were high and may have adversely affected forage quality. Forage utility would be limited to a few months during the growing season.

Atriplex suckleyi (Torrey) Rydb., commonly called rillscale, is the dominant native invader on bentonite mine spoil (Sieg et al. 1983). Rillscale is a spreading annual plant, usually less than 30 cm in height, that flowers from early June to mid-August, bearing mature seed before the end of July. The plant is found only in southern Saskatchewan, southern Alberta, Montana, Wyoming, North Dakota, South Dakota, and Nebraska. It has been observed that the plant grows in saline, clayey, and alkaline land "where nothing else seems to grow" (Frankton and Bassett 1970). Little in known about the biology of this species.

Forage quality is an important consideration in the selection of species for use in revegetation of bentonite mine spoil, since grazing is the major postmining land use in regions where bentonite is mined. Wildlife forage and habitat are also emphasized in reclamation efforts. Twenty-two species of wildlife are known to use *Atriplex* species for food and cover (Robinette 1971, Martin et al. 1951). *Atriplex* species are valued by range managers because of their high protein content (Bidwell and Wooton 1925).

The peak forage value of rillscale, as with most annual forbs, is in all likelihood limited to spring and early summer months (Cook 1972, Stoddart et al. 1975). When available, it may make an important contribution to the nutrition of livestock and wildlife. The objective of this study was twofold: (1) to examine chemical properties of rillscale foliage collected from plots on raw bentonite spoil and on bentonite spoil that had been amended with various combinations of gypsum, fertilizer (NPK), and sawdust during the year prior to harvest; and (2) to assess the effects of treatments on growth of rillscale during the year following treatment.

METHODS

Study Area and Treatments

The study area is located just west of the central Black Hills near Upton, Wyoming, on the Mowry shale formation. Sagebrush (*Artemisia tridentata*) is the predominant vegetation on this grassland, with scattered stands of ponderosa pine (*Pinus ponderosa*). Annual precipitation averages 350 mm (National Oceanic and Atmospheric Administration 1981), falling mostly during the growing season from May to September. Soils are generally shallow and poorly developed.

An area was selected on unreclaimed bentonite mine spoil that was mined before 1968 on the property of American Colloid. The experimental design was that of a 2^3 factorial arrangement of treatments with each of three spoil amendments at two levels (Voorhees et al. 1987). One level was the absence of each amendment, while the other level was the presence of the amendment.

The study site was rototilled to a depth of approximately 5 cm, and gypsum was applied at a level of 31 metric tons per hectare. Introduction of Ca^{++} in the form of $CaSO_4$ was intended to facilitate exchange with monovalent sodium, which would encourage flocculation and water penetration (Brady 1974) and discourage surface crust formation. Fertilizer was added at the rate of 114 kg nitrogen, 23 kg phosphorus, and 50 kg potassium per hectare. Nitrogen and phosphorus were added as ammonium nitrate (NH_4NO_3) and diammonium phosphate ($(NH_4)_2HPO_4$). Potassium was added as potassium chloride (KCl). Sawdust was added at the ratio of one part sawdust to two parts spoil (by volume). Inorganic nitrogen (NH_4NO_3) corresponding to 0.6% of sawdust (by weight) was added to the sawdust before mixing with spoil to prevent a large increase in the carbon-to-nitrogen ratio and subsequent tie-up of soil nitrogen by microorganisms (Allison 1965). This amount of nitrogen corresponded to 6 kg nitrogen per metric ton of sawdust. The sawdust amendment was intended to increase structural stability and tilth of spoil as well as air and water permeability (Voorhees et al. 1983, 1987). The effects of organic matter additions in the form of sawdust might be expected to increase the stability of the substrate where organic matter is less than 2% (Marshall and Holmes 1979) as in bentonite mine spoil (Uresk and Yamamoto 1986).

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Gypsum and sawdust amendments were manually incorporated into tilled spoil, whereas the fertilizer amendment was applied to the surface. All eight combinations of the three amendments, including control, were replicated twice to give a total of 16 plots, each 60 × 150 cm. The plots were tilled, amended, and seeded on 8 May 1982. Plots were self-seeded in 1983 as no seed was planted that year.

Rillscale seed, obtained from sites along the Montana-Wyoming border during late summer of 1980, was planted in each plot so that seed weights corresponded to approximately three live seeds per cm^2. This weight of seed was calculated from total percentage germination and seed density determinations made within six weeks of planting. Seed was broadcast on the surface and raked (1 cm) into spoil.

One-half of each plot was harvested for chemical analysis by manually cutting off stems at ground level during estimated peak standing crop (7 July 1983). The other half was harvested approximately six weeks after estimated peak standing crop (17 August 1983) to determine the rate of decline in standing crop resulting from drying and shattering of foliage as the season progressed. It was assumed that harvesting one-half of each plot had an insignificant effect on plants on the remaining half. All harvested biomass was oven-dried at 55 C, weighed, and ground through a 20-mesh screen.

Plant Tissue Analyses

Plant tissue analyses included total nitrogen by conventional micro-Kjeldahl, in-vitro, dry-matter digestibility, and percentage ash (Church and Pond 1978). Duplicate samples of plant tissue were analyzed to determine nitrogen, ash, and dry-matter digestibility. Dry-matter digestibility was determined with acid pepsin using two 48-hour digestions in a rumen buffer solution taken from cattle eating grass hay (Tilley and Terry 1963). Crude protein percentage was estimated from Kjeldahl nitrogen ($CP = N\% \times 6.25$). Digestible energy (DE) was estimated from dry-matter digestibility values (Rittenhouse et al. 1971) and converted to metabolizable energy (ME) (Mcal/kg dry matter) using the following formula (Swift 1957):

$$DE(Mcal/kg) \times 0.79 = ME(Mcal/kg).$$

Elemental concentrations of nitric acid–extractable aluminum, arsenic, barium, boron, cadmium, calcium, chromium, copper, iron, magnesium, manganese, molybdenum, nickel, phosphorus, potassium, selenium, sodium, strontium, titanium, and zinc were determined for the plant tissue. Samples were analyzed in duplicate; checks (standards) and blanks were included. Elemental concentrations of nitric acid extracts were measured using inductively coupled plasma atomic emission spectrometry (ICP-AES) (Fassel and Knisely 1974, Jones 1977) on the nitric acid digestion (Havlin and Soltanpour 1980, Gestring and Soltanpour 1981).

Statistical Analysis

A three-way factorial analysis of variance was used to determine the effects of spoil amendments (gypsum, sawdust, and fertilizer) and associated interactions on each foliage property. Significant differences were accepted at the .05 probability level.

TABLE 1. Chemical composition of the foliage of rillscale grown on bentonite mine spoil averaged across treatment that did or did not include amendment with sawdust, NPK fertilizer, or gypsum.

	Sawdust		NPK		Gypsum	
Property (units)	without	with	without	with	without	with
Standing crop (kg/ha)	955*[1]	1,973	1,297	1,631	1,534	1,394
Dry-matter digestibility (%)	73	72	73	72	73	73
Digestible energy (kcal/kgDM)[2]	2,968	2,923	2,970	2,920	2,954	2,955
Metabolizable energy (Mcal/kgDM)	2.35	2.31	2.35	2.31	2.32	2.33
Kjeldahl nitrogen (%)	1.70*	1.87	1.74*	1.83	1.74	1.83
Crude protein (%)	11*	12	11	12	11	12
Ash (%)	42*	35	40	37	38	39
Ca (%)	0.47	0.43	0.45	0.45	0.43	0.47
Mg (%)	0.99	0.92	0.98	0.94	0.96	0.95
P (%)	0.19	0.17	0.18	0.18	0.18	0.18
Ca:P	2.55	2.57	2.65	2.47	2.47	2.64
Na (%)	8.55	8.18	8.30	8.43	8.63	8.11
K (%)	1.13	1.10	1.11	1.12	1.12	1.11
Zn (μg/g)	66	63	61	68	55	74
Fe (μg/g)	10,775	11,128	9,924	8,188	3,999	10,775
Mn (μg/g)	496	297	450	343	332	461
N (μg/g)	8	6	8	7	7	8
Cr (μg/g)	5	5	5	5	5	5
Cu (μg/g)	7*	6	6	6	6	7
Mo (μg/g)	16	17	21	13	17	16
Cu:Mo	0.5	0.5	0.5	0.4	0.4	0.5
B (μg/g)	35*	41	37	39	39	37
Al (μg/g)	1,296*	1,006	1,176	1,126	938*	1,365
Ba (μg/g)	37	32	35	34	28	41
Sr (μg/g)	69	73	72	69	68	73
Ti (μg/g)	10	8	9	9	8*	10

[1] Means for each property that are followed by an asterisk (*) are significantly different ($p > .05$).

[2] Based on in-vitro, dry-matter digestibility.

RESULTS

Peak standing crop averaged 1,464 kg dry matter per hectare (Table 1) and ranged from 267 to 2,913 kg dry matter per hectare. Peak standing crop was 107% greater and ash averaged 17% lower on plots that had been amended with sawdust (alone or in combination with other amendments) than on plots that had not been amended with sawdust. Standing crop decreased without grazing by 21% from early July to mid-August.

Digestible energy of rillscale foliage at peak of standing crop (based on IVDMD) was 2,948 kcal/kg dry matter (Table 1). Digestibility of dry matter and estimates of digestible and metabolizable energy levels were all significantly decreased when sawdust and fertilizer were used in combination (with or without the gypsum amendment) relative to the use of other combinations of amendments.

Crude protein of rillscale foliage ranged from 9 to 14%. Amendment of spoil with sawdust (alone or in combination with other amendments) significantly increased the concentration of nitrogen in foliage from 1.70 to 1.87% and increased the crude protein rating from 11 to 12% relative to foliage on spoil not amended with sawdust (Table 1).

Calcium and magnesium levels in rillscale foliage averaged 0.45 and 0.96%, respectively (Table 1). The level of phosphorus was 0.18%, and the ratio of calcium to phosphorus was 2.6:1. Levels of sodium and potassium in rillscale foliage were 8.37 and 1.12%, respectively. When sawdust and fertilizer amendments were used in combination (with or without the gypsum amendment), the foliar content of magnesium and potassium decreased relative to concentrations in foliage on spoils amended with either of these two amendments alone.

Zinc levels in rillscale foliage averaged about 65 μg/g (Table 1). Iron and manganese levels were 9,131 and 397 μg/g, respectively. Nickel levels averaged 7 μg/g, whereas chromium levels were 5 μg/g.

The concentration of copper in foliage was 6 μg/g, while molybdenum concentration was 17 μg/g (Table 1). The sawdust amendment (alone or in combination with other amendments) decreased foliar copper from 7 to 6 µg/g but did not significantly alter the ratio of copper to molybdenum.

High levels of aluminum and iron in rillscale foliage caused severe spectral interferences for arsenic and selenium; thus, it was not possible to determine the concentrations of these elements.

Foliar aluminum levels ranged from 1,000 to 1,300 µg/g. The gypsum amendment (alone or in combination with other amendments) significantly increased foliar aluminum levels from an average of 938 to 1,365 µg/g (Table 1) relative to foliage on spoil that had not been amended with gypsum. Amendment of spoil with sawdust (with or without other amendments) resulted in a decrease in the concentration of aluminum in foliage compared with foliage from spoil not amended with sawdust.

Cadmium levels in rillscale foliage were below detection limits (1.0 µg/g) for the ICP-AES procedure. Boron concentrations in foliage averaged 38 µg/g and were significantly greater when sawdust was added to spoil (with or without other amendments) than they were in foliage grown on spoil not amended with sawdust (Table 1).

Barium levels in foliage averaged 35 µg/g, while strontium concentrations averaged 71 µg/g. When sawdust and fertilizer amendments were used in combination (with or without the gypsum amendment), strontium levels were greater than when either of these amendments was used alone.

Titanium concentrations in foliage averaged 9 µg/g and increased by 25% when gypsum was added (with or without other amendments) relative to foliage from spoil not treated with gypsum (Table 1).

The fertilizer amendment (with or without other amendments) had little effect on foliar composition (Table 1) except through interaction with the sawdust amendment.

Discussion

The forage utility of rillscale as an annual forb is probably limited to a few months during the growing season, culminating with peak of growth in late June and rapidly declining thereafter. Late in the growing season most species of forbs fail to meet the protein and energy needs of gestating animals and are considered inadequate as forage after the fruiting stage (Cook 1972, Stoddart et al. 1975).

The quantities of forage available from growth of rillscale on spoil would be inadequate for most grazing uses except during a few months of the year. Standing crop declined by 21% without grazing from early July to mid-August. This decline following maturity was attributed to drying and shattering of foliage. No evidence of grazing by insects was observed. However, rillscale could make an important contribution to the nutrition of livestock and wildlife during the short period of time it is growing and available. Other plant species could be planted with rillscale (Uresk and Yamamoto 1986, Welch 1989) to help meet the nutritional requirements of herbivores.

The sawdust amendment increased standing crop and decreased ash by improving plant-water relations and increasing the availability of nitrogen. Increased availability of water reduces plant requirements for salts; conversely, plants under water stress accumulate other nutrients when nitrogen is limiting (Mengel and Kirkby 1982). Decreases in plant ash as a result of the sawdust amendment would account for significant decreases in plant uptake of copper and aluminum.

The foliage of rillscale at peak standing crop contained adequate digestible energy (based on IVDMD), crude protein percentage, and concentrations of all mineral elements except phosphorus for cattle, sheep, and wild ruminants (National Research Council 1975, 1984, Dean 1980, Stone et al. 1983). The sawdust amendment (either alone or in combination with other amendments) resulted in an increase in the concentrations of nitrogen and crude protein, while addition of both sawdust and fertilizer (with or without the gypsum amendment) decreased dry-matter digestibility and estimated digestible and metabolizable energy.

Phosphorus supplementation would be advisable for animals foraging on bentonite-mined lands revegetated with rillscale. Calcium levels exceeded most dietary requirements of livestock (National Research Council 1975, 1984, Welch 1989) but were marginal for deer (Dean 1980). Adequate fresh water at low salinity levels would also be necessary, since rillscale contains high quantities of sodium and potassium. Toxicities of electrolytes are considered unlikely unless water intake is restricted or water is highly saline (Church and Pond 1978). Iron, manganese, and aluminum were also present in very high concentrations in the foliage of rillscale, which may depress cellulose digestion (National Research Council 1984, Martinez and Church 1970, Grace 1973). Amendment of spoil with gypsum increased, whereas addition of sawdust decreased, the concentration of foliar aluminum, an important consideration because aluminum can cause gastrointestinal irritation or produce rickets by interfering with phosphate absorption if present in large quantities in the diets of some animals (Underwood 1977). Finally, the copper-to-molybdenum ratio of the foliage of rillscale was low at 0.7 and could cause molybdenum-induced copper deficiencies in livestock and wildlife that do not have access to copper supplements or forages high in copper concentration (Miltmore and Mason 1971, Stone et al. 1983). Other micro- and macro-minerals were adequate to meet the requirements of most herbivores.

The fertilizer treatment (with or without other amendments) had little effect on foliage composition, except through an interaction with the sawdust amendment. The fertilizer amendment may have been ineffective for increasing the availability of nitrogen, phosphorus, and potassium in spoils, or other conditions may have inhibited uptake of these ions. Added nutrients were probably not leached below rooting depth since permeability of unamended spoil is extremely low. Loss of fertilizer as runoff may have been a factor and thus would explain the interaction between fertilizer and sawdust amendments, since sawdust amendment has been shown to increase infiltration and decrease runoff (Voorhees 1986). Alternately, these elements might not have been limiting to plant growth. The latter hypothesis seems unlikely because the sawdust amendment was effective for increasing the level of foliar nitrogen.

Rillscale would be a good choice to consider in revegetating bentonite mine spoils because it provides substantial quantities of forage and nutritional qualities generally adequate to meet requirements of livestock and wildlife. For the few nutritional inadequacies and toxicities of rillscale, introduction of other plants on bentonite spoils may be feasible. Also, grazing native vegetation of the surrounding area should be encouraged.

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SUMMER FOOD HABITS OF COYOTES IN IDAHO'S RIVER OF NO RETURN WILDERNESS AREA

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ABSTRACT.—Summer food habits of coyotes (*Canis latrans*) in the River of No Return Wilderness Area, Idaho, were determined. Analysis of 51 scats (fecal samples) revealed that Columbian ground squirrels (*Spermophilus columbianus*), mule deer (*Odocoileus hemionus*), and deer mice (*Peromyscus maniculatus*) exhibited the greatest frequency of occurrence for identified food items, being detected in 57%, 27%, and 16%, respectively, of scats examined.

One of the most ubiquitous and adaptable predators of the American West is the coyote (*Canis latrans*). As man altered habitats in the western states, the coyote adapted its behavior and diet to take advantage of these new environments. Being generally dietary opportunists (Johnson and Hansen 1977), coyotes have found prey to their liking on man's rangeland (Murie 1951, Short 1979, Green and Flinders 1981) and farms (Gipson 1974), and in his cities (MacCracken 1982). Although many aspects of coyote ecology in man-altered or man-impacted areas of the West have been investigated, less is known of the role of the coyote in relatively undisturbed wilderness. The objective of this study was to determine the summer food habits of coyotes in Idaho's River of No Return Wilderness Area (RNRWA).

STUDY AREA AND METHODS

The study was conducted in the Big Creek Ranger District, RNRWA (formerly the Idaho Primitive Area). A description of the RNRWA and Big Creek area has been provided by Hornocker (1970).

Canid scats were collected from trails located in the Big Creek drainage of the RNRWA. Trails were surveyed the beginning of May 1977 and 1978, and all scats encountered were removed. After the initial clearing, trails were surveyed at least once a month for newly deposited scats. Scat collection concluded at the end of August 1977 and 1978. Collected scats were air-dried and weighed, and diameter at the widest point was determined. Using criteria established in other western studies (Weaver and Fritts 1979, Green and Flinders 1981, Danner and Dodd 1982), we classified all scats ≥ 20 mm in diameter as coyote. Scats were washed, separated, and prepared for analysis in a manner similar to that described by Johnson and Hansen (1979). Prepared scats were analyzed following the procedure of Green and Flinders (1981). Hair was identified by medullary characters (Moore et al. 1974). Teeth were also used to verify the animal species consumed. Each coyote scat was treated as an individual observation. No attempt was made to determine the density of potential prey items in the Big Creek area; hence, it was not possible to determine preference indices for the items identified in the scats examined.

RESULTS AND DISCUSSION

Fifty-one scats collected met the ≥ 20-mm-diameter criterion and were classified as coyote. The average dry weight (± SD) of individual coyote scats was 15.3 ± 5.9 g. Soluble endogenous material accounted for an average 3.9 ± 2.3 g (25%) of dry weight/scat. Thirteen mammal species were identified as food items consumed by coyotes during the summer in the RNRWA (Table 1). Percent occurrence of identified food categories was as follows: rodents 100%, Cervidae 41.4%, insects 39.2%, birds 27.4%, reptiles 3.9%,

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Table 1. Percent occurrence of material identified in 51 coyote scats, River of No Return Wilderness Area, Idaho, May–August 1977 and 1978.

	Month				
Species identified	May (9)[1]	June (14)	July (15)	August (13)	Total (51)
Columbian ground squirrel (*Spermophilus columbianus*)		42.9	73.3	92.3	56.8
Mule deer (*Odocoileus hemionus*)	33.3	35.7	13.3	30.7	27.4
Deer mouse (*Peromyscus maniculatus*)	22.2	14.2	20.0	7.6	15.6
Moose (*Alces alces*)	33.3	21.4		7.6	13.7
Northern pocket gopher (*Thomomys talpoides*)	11.1	14.2	20.0		11.7
Montane vole (*Microtus montanus*)	22.2	21.4	6.6		11.7
Golden-mantled ground squirrel (*Spermophilus lateralis*)	22.2		6.6		5.8
Audubon's cottontail (*Sylvilagus audubonii*)	11.1			7.6	3.9
Horse (*Equus caballus*)	11.1	7.1			3.9
Long-tail weasel (*Mustela frenata*)		7.1			1.9
Northern water shrew (*Sorex palustris*)		7.1			1.9
Water vole (*Arvicola richardsoni*)		7.1			1.9
Snowshoe hare (*Lepus americanus*)		7.1			1.9
Unknown Mammals		7.1	13.3		5.8
Reptiles	22.2				3.9
Arthropods	11.1	21.4	53.3	61.5	39.2
Birds	11.1	7.1	33.3	53.8	27.4
Plant matter	11.1	7.1	40.0	23.0	21.5

[1] Number of scats examined

domestic livestock 3.9%, and other carnivores 1.9%. The results of this study correspond favorably with those of Ribic (1978), Johnson and Hansen (1979), and Short (1979), in that rodents were the most frequently identified food category in the summer diet of western coyotes.

The Columbian ground squirrel (*Spermophilus columbianus*) was the most frequently occurring food item identified in summer coyote scats, being found in 29 (56.8%) of the 51 scats examined. The percent occurrence of Columbian ground squirrel remains in summer scats reflects the seasonal availability of the squirrel as a prey item. *Spermophilus columbianus* within the RNRWA emerge from hibernation in late May and remain active above ground until late August–early September (Elliott and Flinders 1980). The seasonal importance of Columbian ground squirrels as a prey species for other predators (i.e., mountain lions [*Felis concolor*]) in the RNRWA was noted by Seidensticker et al. (1973). Increased mountain lion activity during the day in summer was felt to be related to the availability of Columbian ground squirrels as a food item (Seidensticker et al. 1973). The presence of lesser species in the summer diet of lions was thought to hold down any increases over the lion's winter kill rate of elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) (Hornocker 1970).

Although coyotes and mountain lions utilize a common food resource, it is doubtful that they are serious summer dietary competitors. Elk and mule deer are the major food items consumed by mountain lions during the summer in the RNRWA (Hornocker 1970), whereas rodents comprise the bulk of summer items consumed by coyotes (see Table 1). In the hierarchy of predators in the RNRWA, the coyote appears to occupy a trophic level below that of the mountain lion.

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INFECTION OF YOUNG DOUGLAS-FIRS BY DWARF MISTLETOE IN THE SOUTHWEST

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Abstract.—Studies in several areas in Arizona and New Mexico show that dwarf mistletoe (*Arceuthobium douglasii*) is rare in young Douglas-firs growing under infected overstories. Less than 5% of the Douglas-firs under 26 years old and less than 6% of those under 1.4 m tall were infected in 77 mistletoe-infested stands. Both percent infection and mean dwarf mistletoe rating of young Douglas-firs increased as tree age, height, and stand dwarf mistletoe ratings increased.

Douglas-fir dwarf mistletoe (*Arceuthobium douglasii* Engelm.) is the most prevalent and damaging disease agent in southwestern mixed-conifer forests (Andrews and Daniels 1960, Hawksworth and Wiens 1972, Jones 1974). This parasitic flowering plant occurs throughout the range of its principal host, Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), in the Southwest. Andrews and Daniels (1960) estimated that approximately 50% of the Southwest's Douglas-fir type was infested by dwarf mistletoe.

Douglas-fir regeneration is a frequent component of the understory of southwestern mixed-conifer stands (Moir and Ludwig 1979, Gottfried and Embry 1977, Fitzhugh et al. 1987). When overstories are infested with dwarf mistletoe, spread to young and advance regeneration perpetuates the infestation over time. Therefore, management of mixed-conifer forests should attempt to minimize the infection of new and established regeneration from already infested overstories (Jones 1974, Gottfried and Embry 1977).

Mathiasen (1986) summarized previous research on this problem and the factors that influence dwarf mistletoe infection; he also provided some preliminary information on infection of young Douglas-firs and spruces in the Southwest. He found that little infection of Douglas-fir occurs before saplings are 26 years old. Only 6% of the Douglas-firs he sampled that were less than 26 years old were infected, whereas infection of older Douglas-fir reproduction averaged 83%. Mathiasen (1986) also related infection of Douglas-firs less than 26 years old to three factors affecting infection of young trees listed by Wicker (1967). These included exposure time, overstory inoculum levels, and sapling density.

During a study designed to collect growth data for the development of a regeneration model for southwestern mixed-conifer stands, additional data on the infection of young Douglas-firs were collected from 13 mistletoe-infested stands in the White Mountains, Arizona. These data were combined with the original data collected by Mathiasen (1986), and the results are reported here. In addition, the entire data set was summarized using the heights of sampled Douglas-firs because previous investigators have suggested that height may be a critical factor influencing infection of young trees by dwarf mistletoes (Graham 1960, Hawksworth 1961, Childs 1963, Wicker and Shaw 1967, Scharpf 1969).

Methods

During 1980–81 Douglas-fir regeneration was sampled in 64 mistletoe-infested mixed-conifer stands in four national forests in Arizona and New Mexico. A total of 364 Douglas-fir saplings were sampled for total age, height, and height to live crown. In addition, each Douglas-fir was examined for dwarf mistletoe infection and assigned a dwarf mistletoe rating (DMR) using the 6-class system (Hawksworth 1977). This rating system divides the live crown of a tree into thirds, and each third is rated separately as: 0, no mistletoe infection; 1, less than 50% of live branches infected; 2, more than 50% of live branches infected. The ratings for each third are totaled to obtain the DMR for a tree. Mean stand DMR and mean sapling DMR are calculated by adding the DMRs for all live overstory trees or saplings and dividing by the total number of live trees or saplings, respectively. Infection intensity is defined here as the mean DMR of the overstory or saplings in a stand.

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Overstory data collected for the 1980–81 stands were from rectangular plots ranging from 0.04 to 0.36 ha. For each live tree over 1.4 m in height the species, diameter at breast height (dbh) to the nearest 2.54 cm, DMR, and crown class (dominant, co-dominant, intermediate, or suppressed) were recorded. These data provided information on overstory dwarf mistletoe infection intensity, species composition, and stand structure.

In 1988 an additional 334 Douglas-fir saplings were sampled in 13 mistletoe-infested, mixed-conifer stands in the White Mountains, Arizona. Data were collected as in 1980–81. Overstory data collected were the same as in 1980–81 but 0.04-ha circular plots were used.

Stand dwarf mistletoe ratings were calculated using all live Douglas-firs greater than 2.54 cm dbh for 1980–81 plots and greater than 5.08 cm dbh for 1988 plots. Sapling crown ratios were calculated by subtracting height to live crown from total height and then dividing by total height. Percent infection and mean DMR for saplings were calculated by five-year age classes and .3-m height classes for each of three stand DMR classes (0.1–1.5, 1.6–3.0, and greater than 3.0). Sapling densities were determined for the number of Douglas-fir saplings in 0.04-ha circular subplots nested in the center of larger plots in each stand.

RESULTS

Both the number of infected saplings (percent infection) and infection intensity (mean DMR) increased as total age, total height, and stand DMR increased (Tables 1 and 2). No mistletoe infection was found on saplings under 21 years old in stands with a stand DMR less than 3.0, and only five saplings under 21 years old were infected in stands with a stand DMR greater than 3.0 (Table 1). The five infected saplings represent less than 4% of saplings under 21 years old sampled. Infection of saplings less than 16 years old was only 2% in stands with a stand DMR greater than 3.0. Also, very little infection of saplings less than 26 years old was found (Table 1). Only 10% of saplings 21–25 years old were infected, and all were in moderately infested (stand DMR 1.6–3.0) or severely infested stands (stand DMR greater than 3.0).

Infection of 26–30-year-old saplings increased to 30% in lightly infested stands (stand DMR 0.1–1.5) and to over 65% in both moderately and severely infested stands (Table 1). Generally, infection continued to increase as sapling age increased (Table 1).

A total of 14 infected saplings under 26 years old were sampled. These saplings were in severely infested stands, were over 1.4 m in height, had high crown ratios (greater than 0.70), or were in stands with over 740 saplings per ha. Many of these 14 saplings had more than one of the above factors contributing to their infection potential.

Percent infection and mean DMR for saplings demonstrated the same pattern for height classes as for age classes (Tables 1, 2). Little infection (10% or less) was found in saplings less than 1.4 m in height, except in the most severely infested stands, where we found 27% infection in saplings 1.09–1.4 m tall. However, saplings over 1.4 m in height had much higher infection levels (percent infection) and intensities (mean DMR) than smaller saplings (Table 2).

DISCUSSION

Wicker (1967), Wicker and Shaw (1967), and Mathiasen (1986) discussed several of the factors influencing the infection of young trees by dwarf mistletoes, including duration of exposure to inoculum, amount of inoculum, target area, density of regeneration, and removal of seeds by wind, snow, and other environmental factors. Infection of susceptible young trees is largely influenced by a complex interaction of the above factors. Mathiasen (1986) presented information on the influence of exposure duration to inoculum (as expressed by tree age), amount of inoculum (as expressed by stand DMR), and regeneration density (as expressed by number of saplings per ha). Additional information is reported

TABLE 1. Infection of Douglas-fir saplings by age classes and stand DMR classes.

	Stand DMR class											
	0.1–1.5			1.6–3.0			> 3.0			Total		
Age class (years)	N	% Inf[1]	Mean DMR	N	% Inf	Mean DMR	N	% Inf	Mean DMR	N	% Inf	Mean DMR
< 16	49	0	0.0	58	0	0.0	108	2	<0.1	215	1	<0.1
16–20	30	0	0.0	29	0	0.0	21	14	0.1	80	4	<0.1
21–25	15	0	0.0	43	9	<0.1	35	14	0.1	93	10	<0.1
26–30	27	30	0.3	38	79	0.8	35	69	0.7	100	62	0.6
31–35	8	25	0.3	39	80	1.1	41	88	0.9	88	78	0.9
36–40	12	66	0.9	40	90	1.4	36	97	1.8	88	90	1.5
41–45	7	71	0.9	15	80	2.0	12	100	2.8	34	85	1.9
Total	148	16	0.2	262	43	0.6	288	41	0.6	698	36	0.5

[1] Percent infection

TABLE 2. Infection of Douglas-fir saplings by height classes and stand DMR classes.

	Stand DMR class											
	0.1–1.5			1.6–3.0			> 3.0			Total		
Height class (m)	N	% Inf[1]	Mean DMR	N	% Inf	Mean DMR	N	% Inf	Mean DMR	N	% Inf	Mean DMR
.15–.45	23	0	0.0	20	0	0.0	45	0	0.0	88	0	0.0
.46–.76	14	0	0.0	13	0	0.0	35	3	<0.1	62	2	<0.1
.77–1.07	21	5	<0.1	33	0	0.0	31	6	0.1	85	4	<0.1
1.10–1.37	21	5	0.2	29	10	0.1	22	27	0.2	72	14	0.2
1.40–1.68	15	27	0.4	44	61	1.2	32	66	1.3	91	57	1.0
1.71–1.98	15	40	0.7	48	65	1.5	41	71	1.6	104	64	1.4
2.01–2.29	9	44	0.6	23	70	1.4	24	75	2.0	56	68	1.3
< 2.29	30	23	0.6	52	70	1.2	58	69	1.8	140	59	1.4
Total	148	16	0.2	262	43	0.6	288	41	0.6	698	36	0.5

[1] Percent infection

here for these factors as well as for the influence of target area as expressed by the total height and crown ratio of young infected Douglas-firs. In most situations where infected young Douglas-firs (less than 26 years old) were found, a severely infested overstory (stand DMR greater than 3.0) was present. Infected young Douglas-firs in stands with a stand DMR less than 3.0 either had high crown ratios (greater than 0.70), were over 1.4 m tall, or were in stands with regeneration densities over 740 saplings per ha. All three factors would increase the potential for infection of young trees in dwarf mistletoe–infested stands because of greater available target area.

Because severe infection by dwarf mistletoe significantly reduces the growth of merchantable-size Douglas-firs in the Southwest and increases mortality of all size classes (Andrews and Daniels 1960, Mathiasen et al. 1990), its control is an important consideration for resource managers. Vegetation management plans that do not successfully prevent or significantly reduce the infection of Douglas-fir regeneration only serve to perpetuate mistletoe infestations. Although the total heights, crown ratios, and densities of regeneration contribute to the potential for reinfection of young understories, these factors cannot be managed on a practical basis. However, management plans that remove the most severely infected trees, followed with intermediate sanitation removals, can effectively reduce the level of dwarf mistletoe infection in stands (Hawksworth 1978), thereby reducing the potential for infection of new or advance regeneration. In addition, because Douglas-fir regeneration is not frequently infected before it reaches ages over 25 years in the Southwest, cutting cycles of 20 years or less allow managers at least two management entries for reducing the level of mistletoe in a stand before new Douglas-fir regeneration will be affected. Because little or no infection will occur until Douglas-firs are over 20 years old in lightly infested stands, the removal of severely infected overstory trees will significantly reduce the potential for infection of new and advance Douglas-fir regeneration.

The age at which Douglas-fir regeneration becomes infected by dwarf mistletoe in the Southwest contrasts sharply with results reported for other tree species and regions. Weir (1918) found that the average age of 50 naturally infected Douglas-fir seedlings, used for assessing the effects of dwarf mistletoe on seedling growth in the Northwest, was 18 years. Hawksworth and Graham (1963) found very little infection in lodgepole pine (*Pinus contorta* Dougl. ex Loud.) reproduction under 10 years old, but infection increased markedly in older stands: 9% at age 15, 18% at age 20, and 32% at age 25. Some infection of ponderosa pine (*Pinus ponderosa* Laws.) by southwestern dwarf mistletoe (*Arceuthobium vaginatum* subsp. *cryptopodum* [Engelm.] Hawksw. & Wiens) has been found in 10-year-old seedlings (Gill and Hawksworth 1954, Hawksworth 1961). Based on these findings for pines, Johnson and Hawksworth (1985) recommended that mistletoe-infected residual trees be removed before the young stand is 10 years old. However, the results of this study indicate that for southwestern Douglas-fir the infected overstory trees could be left for up to 20 years because of the very slight chance of infection.

There is less published data for the relationship of regeneration height and dwarf mistletoe infection, but the general recommendation is that mistletoe-infected residual trees should be removed before the young stand is 0.9 m tall (Johnson and Hawksworth 1985). Graham (1960) found that dwarf mistletoe infection in Douglas-fir increased as size class increased in northern Idaho: Only 15% of the saplings sampled by Graham were infected, whereas 25 and 39% of the small and large poles, respectively, were infected.[3] Hawksworth (1961) reported that 19% of the ponderosa pines in the 2.54-cm-diameter class were infected in stands infested by southwestern dwarf mistletoe in northern Arizona, but infection increased to 57% in the 12.7-cm-diameter class. Childs (1963), working in the Pacific Northwest, found that uninfected ponderosa pines averaged 1.5 and 1.1 m in height in lightly and heavily mistletoe-infested stands, respectively, and infected pines averaged 2.3 and 2.0 m in the same stands. Scharpf (1969) reported that only 7% of true firs under 0.9 m tall were infected in severely infested stands in California but that infection intensified rapidly in taller regeneration. The results of infection of Douglas-firs by height classes reported here indicate that little infection can be expected until the trees reach heights greater than 1.4 m in the Southwest.

Because these findings have important implications in managing dwarf mistletoe–infested stands, similar studies should be conducted for other dwarf mistletoe–host combinations in other regions of the western United States. The results show that the generally accepted recommendation that infected overstory pines and true firs be removed before the young stand is 10 years old or 0.9 m tall is more restrictive than need be for Douglas-fir in the Southwest, where little infection occurred in stands under 20 years old or less than 1.4 m tall.

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NEW MEXICO GRASS TYPES AND A SELECTED BIBLIOGRAPHY OF NEW MEXICO GRASS TAXONOMY[1]

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ABSTRACT.—Collection data, bibliographic citations, and curatorial information on 52 names of New Mexico grass types are compiled. A bibliography of taxonomic research pertinent to the study of New Mexico grasses is cross-referenced with genera known to occur in the state.

Bibliographic and historical information are an essential, but often neglected, resource for the student of plant systematics. The correct application of plant names requires accurate information concerning nomenclatural types, and precise floristic and identification work demands access to reliable monographic or revisionary literature. This is especially so when changes are made in traditional systematic alignments; reference literature allows others to understand and evaluate the revisions.

Nearly every botanist engaged in the taxonomy of grasses (Gramineae) during the past century described at least one novelty from New Mexico material. The list of grass types presented here includes 52 taxa known to have been described from specimens gathered in New Mexico. As a point of comparison, 19 grass taxa have been named from Utah material (Welsh 1982). Twenty-one different authors contributed new taxa; but three, George Vasey (14 names), John Torrey (6 names), and Ernst Steudel (5 names), accounted for nearly 50% of the plant names (Table 1). Botanical publication of grass taxa from New Mexico began in 1854 with species of *Aristida*, *Muhlenbergia*, *Oryzopsis*, and *Poa* (Steudel 1854) and has continued for well over a century, the latest being in 1986 from the genus *Andropogon* (Campbell 1986). Of the authors, only A. S. Hitchcock, Paul Standley, George Thurber, George Vasey, and E. O. Wooton also participated as field collectors of new grasses from New Mexico (Table 1). George Vasey heads the list with collections of 9 new taxa from New Mexico. Grant and Santa Fe counties contain the most localities of new grasses (Table 2). Santa Fe is one of the oldest towns in the United States and was visited by many collectors early in the 1800s. William Gambel passed through in 1841 or 1842 on his way to California; his collections were described by Thomas Nuttall. Wislizenus followed in 1846. August Fendler made extensive collections there in the spring of 1847, sending them to Asa Gray. Most of his collections came from the Santa Fe Creek area and within 10–12 miles of Santa Fe. A. A. Heller, G. R. Vasey, S. M. Tracy, and T. D. A. Cockerell were other botanists who collected near Santa Fe in the late 1800s or early 1900s; the collections of Vasey and Tracy contributed new grasses. Many of the collections from Grant County came from the mining camp of Santa Rita, 15 miles east of Silver City. Charles Wright, J. M. Bigelow, and George Thurber collected there in the 1850s. Mangas Springs, also in Grant County, was visited by O. B. Metcalfe in 1903, who collected several hundred sets of plants. C. G. Pringle, H. H. Rusby, and J. G. Smith also collected new grasses from Grant County (Standley 1910).

The ensuing list attempts to include all grass names based on New Mexico material. The author of the name, publication data, collector and number, locality of collection, deposition of type material, and current taxonomic disposition of the name are given for each type.

Following the list of types is a list of the

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[1] Journal Article 1474, New Mexico Agricultural Experiment Station, Las Cruces.

[2] Department of Animal and Range Sciences, Box 3-I, New Mexico State University, Las Cruces, New Mexico 88003.

TABLE 1. Authors and collectors of New Mexico grass types.

Name	Authored	Collected
Thomas Antisell	0	1
William J. Beal	1	0
John M. Bigelow	0	5
W. S. Boyle	1	0
Samuel B. Buckley	2	0
Christopher S. Campbell	1	0
Karel Domin	2	0
William H. Emory	0	1
August Fendler	0	7
William Gambel	0	2
Eduard Hackel	1	0
Albert S. Hitchcock	2	2
Edwin James	0	1
Ivan M. Johnston	1	0
Marcus E. Jones	1	0
O. C. Louis-Marie	1	0
Edgar A. Mearns	0	1
Elmer D. Merrill	1	0
Orrick B. Metcalfe	0	3
George Nash	3	0
Thomas Nuttall	2	0
Cyrus G. Pringle	0	1
H. H. Rusby	0	1
Frank L. Scribner	4	0
Cornelius L. Shear	1	0
Jared G. Smith	1	2
Paul C. Standley	1	1
Ernst G. Steudel	5	0
Jason Swallen	3	0
George Thurber	1	1
John Torrey	6	0
Samuel M. Tracy	0	1
George Vasey	14	9
Wilkins	0	1
S. W. Woodhouse	0	1
Elmer O. Wooton	1	5
Charles Wright	0	6

grass genera of New Mexico cross-referenced to a selected bibliography. The bibliography is not intended to be exhaustive; rather, only significant revisionary or summary papers pertinent to New Mexico grass taxonomy are listed. Further references may be obtained by consulting the works listed here, particularly Gould and Shaw (1983) and Soderstrom et al. (1987).

NEW MEXICO GRASS TYPES

The acronym in parentheses (Holmgren et al. 1981) refers to the locality of type material: holotype, isotype, fragment, or other duplicate material.

Agrostis minutissima Steudel, Syn. Pl. Glum. 1: 171. 1854. Fendler 986, in 1847, Santa Fe Co., near Santa Fe (US). = *Muhlenbergia minutissima* (Steud.) Swallen

TABLE 2. Counties of collection of New Mexico grass types.

County	Number of types
Bernalillo	1
Colfax	1
Doña Ana	4
Eddy	3
Grant	12
Hidalgo	1
Lincoln	1
Otero	2
Rio Arriba	2
San Miguel	3
Santa Fe	11
Socorro	1

Andropogon glomeratus (Walter) B.S.P. var. ***scabriglumus*** Campbell, Syst. Bot. 11: 291. 1986. C. Wright 2100, in 1851, Grant Co., probably near Silver City (GH).

Andropogon neo-mexicanus Nash, Bull. Torr. Bot. Club 25: 83. 1898. E. O. Wooton 583, 26 Aug 1897, Otero Co., White Sands (NY). = *Schizachyrium neomexicanum* (Nash) Nash

Andropogon wrightii Hackel, Flora 68: 139. 1885. C. Wright 2104, in 1851, Grant Co., Silver City (US). = *Bothriochloa wrightii* (Hack.) Henr.

Aristida fendleriana Steudel, Syn. Pl. Glum. 1: 420. 1854. Fendler 973, in 1847, Santa Fe Co., Santa Fe (US). = *Aristida purpurea* Nutt. var. *fendleriana* (Steud.) Vasey

Aristida longiseta Steudel, Syn. Pl. Glum 1: 420. 1854. Fendler 978, in 1847, probably Santa Fe Co., Santa Fe (US). = *Aristida purpurea* Nutt. var. *longiseta* (Steud.) Vasey

Aristida pansa Wooton & Standley, Contr. U.S. Natl. Herb. 16: 112. 1913. Wooton s.n., 6 Oct 1904, Doña Ana Co., Tortugas Mt. near Las Cruces (US).

Aristida subuniflora Nash in Small, Fl. Southeast. U.S. 116. 1903. Vasey s.n., in 1881?, "New Mexico," probably Santa Fe Co. near Santa Fe (NY). = *Aristida purpurea* Nutt. var. *fendleriana* (Steud.) Vasey

Bouteloua pusilla Vasey, Bull. Torr. Bot. Club 11: 6. 1884. G. R. Vasey s.n., "Kingman, New Mexico" (US). [Probably Kingman, Arizona, as there is no known Kingman, New Mexico.] = *Bouteloua simplex* Lag.

Bromus porteri (Coulter) Nash var. ***frondosus*** Shear, U.S.D.A. Div. Agrost. Bull. 23: 37. 1900. J. G. Smith s.n., Grant Co., Mangas Springs (US).

Calycodon montanum Nuttall, J. Acad. Nat. Sci. Phil. n. ser. 1: 186. 1848. W. Gambel s.n., Santa Fe Co., near Santa Fe (PH). = *Muhlenbergia montana* (Nutt.) A. S. Hitchc.

Chaetochloa grisebachii (Fourn.) Scribn. var. ***ampla*** Scribner & Merrill, U.S.D.A. Div. Agrost. Bull. 21: 36. 1900. G. R. Vasey s.n., in 1881, Doña Ana Co., Organ Mountains (US). [One of two specimens cited] = *Setaria grisebachii* Fourn.

Chondrosium eriopodum Torrey in Emory, Notes Mil. Reconn. 154. 1848. Bigelow s.n., in 1847, "along the Del Norte [Rio Grande] River," New Mexico (US). = *Bouteloua eriopoda* (Torr.) Torr.

Chrondrosium foeneum Torrey in Emory, Notes Mil. Reconn. 154. 1848. Emory s.n., in 1847, "uplands bordering the valley of the Del Norte [Rio Grande]." = *Bouteloua hirsuta* Lag.

Epicampes subpatens A. S. Hitchcock, U.S.D.A. Bull. 772: 144. 1920. A. S. Hitchcock 13541, Eddy Co., Guadalupe Mountains (US). = *Muhlenbergia emersleyi* Vasey

Eragrostis fendleriana Steudel, Syn. Pl. Glum 1: 278. 1854. Fendler 932, in 1847, "Mexico" [now New Mexico], probably Santa Fe Co. near Santa Fe (US). = *Poa fendleriana* (Steud.) Vasey

Eragrostis neomexicana Vasey, Contr. U.S. Natl. Herb. 2: 542. 1894. Vasey s.n., in 1881, Doña Ana Co., Organ Mountains (US). = *Eragrostis mexicana* (Hornem.) Link

Fendleria rhynchelytroides Steudel, Syn. Pl. Glum. 1: 420. 1854. Fendler 979, in 1847, probably Santa Fe Co. near Santa Fe (US). = *Oryzopsis hymenoides* (Roem. & Schult.) Ricker

Koeleria macrura Domin forma ***triflora*** Domin, Bibl. Bot. 65: 238. 1907. E. O. Wooton 110, probably 1897, Doña Ana Co., Organ Mountains (US). = *Koeleria macrantha* (Ledeb.) Schult.

Koeleria nitida Nuttall var. ***laxa*** Domin, Bibl. Bot. 65: 235. 1907. O. B. Metcalfe s.n., perhaps Grant Co., "New Mexico." [Another specimen from Arizona also cited] = *Koeleria macrantha* (Ledeb.) Schult.

Melica porteri Scribner var. ***laxa*** Boyle, Madroño 8: 25. 1945. E. O. Wooton 680, in 1897, Lincoln Co., White Mountains (US).

Muhlenbergia abata I. M. Johnston, J. Arnold Arbor. 24: 387. 1943. Wright 1982, in 1851, valley of the Rio Grande (GH). = *Muhlenbergia repens* (Presl) A. S. Hitchc.

Muhlenbergia acuminata Vasey, Bot. Gaz. 11: 337. 1886. Wright 1993, in 1851, probably Grant Co. near Santa Rita (US). = *Muhlenbergia dubia* Fourn.

Muhlenbergia metcalfei M. E. Jones, Contr. West. Bot. 14: 12. 1912. O. B. Metcalfe 1485, in 1904, Grant Co., Santa Rita Mountains (US).

Muhlenbergia neo-mexicana Vasey, Bot. Gaz. 11: 337. 1886. G. R. Vasey s.n., in 1881?, "rocky hills and mountain sides, New Mexico" (US). = *Muhlenbergia pauciflora* Buckl.

Muhlenbergia sinuosa Swallen, Contr. U.S. Natl. Herb. 29: 204. 1947. E. A. Mearns 2457, in 1893, Hidalgo Co., San Luis Mountains (US).

Muhlenbergia sylvatica (Torr.) Torr. var. ***flexuosa*** Vasey in Wheeler, Rpt. U.S. Survey W. 100th Merid. 6: 284. 1878. Wright 731, in 1851, perhaps Grant Co. near Silver City. = *Muhlenbergia monticola* Buckl.

Muhlenbergia sylvatica (Torr.) Torr. var. ***pringlei*** Scribner, Bull. Torr. Bot. Club 9: 89. 1882. C. Pringle 480, Grant Co., Santa Rita Mountains (US). = *Muhlenbergia pauciflora* Buckl.

Muhlenbergia wrightii Vasey in Coulter, Man. Rocky Mount. 409. 1885. Wright 1986, in 1851, "Colorado and New Mexico" (US).

Panicum bulbosum H.B.K. var. ***minus*** Vasey, U.S.D.A. Div. Bot. Bull. 8: 38. 1889. Rusby s.n., in 1880, perhaps Grant Co. near Mangas Springs (US).

Panicum lachnanthum Torrey, U.S. Expl. Miss. Pacif. Rpt. 7: 21. 1858. T. Antisell s.n., in Aug 1854, Grant Co., Burro Mountains (NY). = *Digitaria californica* (Benth.) Henr.

Panicum plenum A. S. Hitchcock & Chase, Contr. U.S. Natl. Herb. 15: 80. 1910. Metcalfe 739, Sep 1903, Grant Co., Mangas Springs (US). = *Panicum bulbosum* H.B.K.

Pleopogon setosum Nuttall, J. Acad. Phil. n. ser. 1: 189. 1848. W. Gambel s.n., in 1841 or 1842, Santa Fe Co., "mountains of Santa Fe" (PH). = *Lycurus phleoides* H.B.K. var. *glaucifolius* Beal

Pleuraphis jamesii Torrey, Ann. Lyc. N.Y. 1: 148. 1824. James s.n., in 1852, sources of the Canadian River, Texas or New Mexico (NY). = *Hilaria jamesii* (Torr.) Benth.

Poa arida Vasey, Contr. U.S. Natl. Herb. 1: 270. 1893. G. R. Vasey s.n., in 1881, Socorro Co., Socorro (US).

Poa bigelovii Vasey & Scribner, Contr. U.S. Natl. Herb. 1: 270. 1893. Fendler 931, in 1847, "New Mexico," Santa Fe Co., probably along Santa Fe Creek east of Santa Fe (US?).

Poa occidentalis Vasey, Contr. U.S. Natl. Herb. 1: 274. 1893. G. R. Vasey s.n., in 1881, Santa Fe Co., near Santa Fe (US).

Poa tracyi Vasey, Contr. U.S. Natl. Herb. 1: 276. 1893. S. M. Tracy s.n., in 1887, Colfax Co., "on mountain sides at Raton" (US).

Sitanion caespitosum J.G. Smith, U.S.D.A. Div. Agrost. Bull. 18: 16. 1899. J. G. Smith s.n., in 1897, Grant Co., near Cliff (US). = *Elymus longifolius* (Smith) Gould

Sporobolus filiculmis Beal, Grasses N. Amer. 2: 288. 1896. Bigelow s.n., Sep 1853, Rio Arriba Co., Plaza Larga. = *Muhlenbergia thurberi* Rydb.

Sporobolus giganteus Nash, Bull. Torr. Bot. Club 25: 88. 1898. E. O. Wooton 394, 26 Aug 1907, Otero Co., White Sands (US).

Sporobolus thurberi Scribner, U.S.D.A. Div. Agrost. Bull. 11: 48. 1898. Bigelow s.n., Sep 1853, Rio Arriba Co., Plaza Larga (US). = *Muhlenbergia thurberi* Rydb.

Stipa curvifolia Swallen, J. Wash. Acad. Sci. 23: 456. 1933. Wilkins 1660, Eddy Co., Guadalupe Mountains (US).

Stipa lobata Swallen, J. Wash. Acad. Sci. 23: 199. 1933. A. S. Hitchcock (Amer. Gr. Natl. Herb. 819), Eddy Co., Queen, Guadalupe Mountains (US).

Stipa pennata L. var. ***neomexicana*** Thurber in Coulter, Man. Rocky Mount. 408. 1885. Thurber 269, probably Grant Co., "Rio Mimbres." = *Stipa neomexicana* (Thurb.) Scribn.

Stipa scribneri Vasey, Bull. Torr. Bot. Club 11: 125. 1884. Vasey s.n., in 1881?, Santa Fe Co., Santa Fe (US).

Tricuspis mutica Torrey, U.S. Expl. Miss. Pacif. Rpt. 4: 156. 1856. Bigelow s.n., 22 Sep 1853, San Miguel Co., Laguna, Colorado (NY). = *Tridens muticus* (Torr.) Nash

Trisetum montanum Vasey, Bull. Torr. Bot. Club 13: 118. 1886. G. R. Vasey s.n., in 1881, San Miguel Co., Las Vegas (US).

Trisetum montanum Vasey var. ***pilosum*** Louis-Marie, Rhodora 30: 212. 1928. P. C. Standley 4536, Aug 1908, San Miguel Co., Cowles. = *Trisetum montanum* Vasey

Uralepis composita Buckley, Proc. Acad. Nat. Sci. Phila. 1862: 94. 1862. Woodhouse s.n., probably 1851, "New Mexico" (PH). = *Leptochloa fascicularis* (Lam.) Gray

Uralepis poaeoides Buckley, Proc. Acad. Nat. Sci. Phila. 1862: 94. 1862. Fendler 932, in 1847, probably Santa Fe Co. near Santa Fe (PH). = *Poa fendleriana* (Steud.) Vasey

Vilfa tricholepis Torrey, U.S. Expl. Miss. Pacif. Rpt. 4: 155. 1857. Bigelow s.n., Oct 1853, Bernalillo Co., Sandia Mountains (NY). = *Blepharoneuron tricholepis* (Torr.) Nash

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Triticeae tribe 18, 19, 23, 38, 39, 41, 77, 78, 79, 151
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NOTEWORTHY MAMMAL DISTRIBUTION RECORDS FOR THE NEVADA TEST SITE

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Previous reports on the mammals of the Nevada Test Site, Nye County, Nevada (Jorgensen and Hayward 1965, O'Farrell and Emery 1976), indicate the presence of 46 species (42 terrestrial mammals and 4 bats).

Under a new project entitled Basic Environmental Compliance and Monitoring Program at the Nevada Test Site, two previously uncollected species of mammals were obtained, and a range extension for a third species was documented during the 1988 sampling season. Voucher specimens have been deposited at the Nevada State Museum in Las Vegas, Nevada.

Mustela frenata nevadensis Hall.— Small-animal trapping was conducted on three consecutive nights in Rock Valley, Nye County, Nevada, elevation 1,035 m. (14–16 June 1988). On 15 June 1988 two *M. f. nevadensis* (an adult female and a juvenile female) were captured in Sherman traps. This record extends the known range on the Nevada Test Site approximately 58 km south of the previous known locality. Prior records reported *M. f. nevadensis* from the vicinity just south of Whiterock Spring in northwestern Yucca Flat in the Grayia-Lycium community (Jorgensen and Hayward 1965). The male *M. f. nevadensis* (4298 BYU) cited by Jorgensen and Hayward (1965) was collected on 15 May 1961, dead on the road, and measured 386-130-41-no ear measurement, no skull (Jorgensen, personal communication). I observed an additional juvenile live specimen in early April 1987 approximately 4 km southeast of Whiterock Spring; it was later released. Additional published records for *M. f. nevadensis* exist for the Spring Mountains, Clark County, Nevada, ~50 km southeast of Rock Valley, where weasels were observed but not collected (Burt 1934), and Arlemont, Esmeralda County, Nevada, 1,478 m, Fish Lake Valley (Hall 1951: 290), which is ~210 km northwest of Rock Valley.

The juvenile female specimen collected in Rock Valley, 36°41′N, 116°11′W, (NSMLV-M-9202) measured 319-110-32-17 and weighed 91 g. It is important to note that Rock Valley lies at the northern edge of the Specter Range along the southern boundary of the Nevada Test Site. The vegetation consists primarily of *Larrea tridentata*, *Lycium andersonii*, *Lycium pallidum*, and *Ambrosia dumosa* (Romney et al. 1973). This region is located in an area that contains no aboveground permanent water source. The nearest source is a "tinaja," a small rock crevice with an opening approximately 20 cm that stores water collected from runoff; it is approximately 5 km west of the locality in which the *M. f. nevadensis* were collected.

Urocyon cinereoargenteus scottii Mearns. — One specimen was collected dead on Holmes Road, 1.3 km northwest of the junction of Holmes Road and Stockade Wash Road, Nevada Test Site, Nye County, Nevada (37°10′N, 116°13′W), at 0700 hr on 2 August 1988. This immature female specimen (NSMLV-M-9203) measured 727-310-120-70 and weighed 1733 g. This location is at the southern end of Rainier Mesa at an elevation of 1,993 m and at the lower edge of pinyon-juniper habitat. Hall (1946:241) cited a trapper capturing gray fox at 2,194 m, 8.9 km northwest of Whiterock Spring during the winter of 1930–31 in pinyon timber. This locality was most likely on the top of Rainier Mesa or Aqueduct Mesa in the Belted Range on the Nevada Test Site. An additional sighting was recorded on Pahute Mesa by

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D. Badger on 29 September 1986, 3.4 km north of Silent Canyon (37°19′N, 116°19′W) along Dead Horse Flats Road, Nevada Test Site, at an elevation of 2,102 m.

This specimen (NSMLV-M-9203) verifies the Hall (1946) record and substantiates Jorgensen and Hayward's (1965) contention that this species would eventually be collected on the Nevada Test Site, which falls within the distribution illustrated by Hall (1981).

Microdipodops megacephalus sabulonis Hall.— Three specimens were captured on Pahute Mesa, 0.3 km north of the junction of Pahute Mesa Road and Buckboard Mesa Road (37° 15′ N, 116° 28′ W) at an elevation of 1,919 m, one on 29 June 1988 and two on 19 August 1988. The two August specimens were preserved and provide the first voucher specimens for the Nevada Test Site, Nye County, Nevada. These specimens measured (NSMLV-M-9200) male, 147-75-25-10, 12 g; (NSMLV-M-9201) female, 150-75-24-10, 13 g. Jorgensen and Hayward (1965) reported collecting three specimens north of the Nevada Test Site in Kawich Valley (BYU 4485, 4486, 4487). Two additional records of *M. m. sabulonis* exist from the Nellis Bombing and Gunnery Range northeast of the Nevada Test Site. One specimen (BYU 4097) was collected 7 km north of the northeast boundary of the Nevada Test Site, and the second record was reported by Bradley and Moor (1975) from 8 km north of the northeast boundary of the Nevada Test Site. The two specimens of *M. m. sabulonis* reported here (NSMLV-M-9200, NSMLV-M-9201) extend the known distribution approximately 32.2 km southwest of Kawich Valley and on to Pahute Mesa on the Nevada Test Site.

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FORMATION OF *PISOLITHUS TINCTORIUS* ECTOMYCORRHIZAE ON CALIFORNIA WHITE FIR IN AN EASTERN SIERRA NEVADA MINESOIL

R. F. Walker[1]

The Gasteromycete *Pisolithus tinctorius* (Pers.) Coker & Couch occurs in temperate, subtropical, and tropical zones worldwide and in ectomycorrhizal association with numerous conifer and hardwood hosts (Marx 1977). Frequent reports of the occurrence of its basidiocarps near various pine species on harsh sites in the eastern United States (Lampky and Peterson 1963, Schramm 1966, Hile and Hennen 1969, Lampky and Lampky 1973, Marx 1975, Medve et al. 1977) have prompted extensive efforts to inoculate seedlings in forest nurseries with this mycobiont (Marx et al. 1976, 1982, 1984, 1989a, 1989b). Subsequently, the improved survival and growth of pine seedlings with *P. tinctorius* ectomycorrhizae after outplanting on surface mines has been attributed to enhanced uptake of nutrients (Marx and Artman 1979) and water (Walker et al. 1989). Current research is focused on development of more effective inocula and inoculation procedures, discovery of locally adapted *P. tinctorius* isolates, and identification of new host species.

A recent report (Walker 1989) disclosed *P. tinctorius* occurring in ectomycorrhizal association with Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) and Sierra lodgepole pine (*Pinus contorta* var. *murrayana* [Grev. & Balf.] Engelm.) on spoils of the Leviathan Mine in Alpine County, California. Located on the eastern slope of the Sierra Nevada (38°42′30″N, 119°39′15″W) at an elevation of 2,200 m and consisting of approximately 100 ha, this open-pit sulfur mine has been inactive since 1962. The average annual precipitation of approximately 50 cm is primarily snowfall, and the minesoil has a pH of 4.0 to 4.5, a deficiency of plant-available N, and a potentially phytotoxic concentration of Al (Butterfield and Tueller 1980). Vegetation is sparse on most of the spoils, but in addition to the two pine species mentioned previously, California white fir (*Abies concolor* var. *lowiana* [Gord.] Lemm.), singleleaf pinyon (*Pinus monophylla* Torr. & Frem.), Utah juniper (*Juniperus osteosperma* [Torr.] Little), and quaking aspen (*Populus tremuloides* Michx.) have become reestablished on the periphery of the mine near adjoining undisturbed forest and woodland. Walker's (1989) report concerning examinations made in September 1988 of the probable hosts of *P. tinctorius* in Leviathan Mine noted that basidiocarps of this symbiont were absent in the immediate vicinity of the latter four tree species.

Reexamination of Leviathan Mine spoils in August and September 1989, however, revealed numerous *P. tinctorius* basidiocarps near seedlings and saplings of California white fir. Typically, one or two dark yellow to brown basidiocarps (Fig. 1A), matching the description of Coker and Couch (1928), were observed around solitary white fir seedlings, while as many as five encircled individual white fir saplings. Stipitate, substipitate, and sessile forms were observed, varying in size from 9 to 17 cm in length and from 3 to 7 cm in diameter. Approximately 100 basidiocarps were found associated with white fir, and these were rarely more than 2 m from the host.

Strands of mycelia with gold-yellow pigmentation, which compare favorably with the *P. tinctorius* rhizomorphs described by Schramm (1966), were traced through the spoils from basidiocarps to the root systems of white fir seedlings and saplings. These mycelia were connected to ectomycorrhizae of similar pigmentation that matched the

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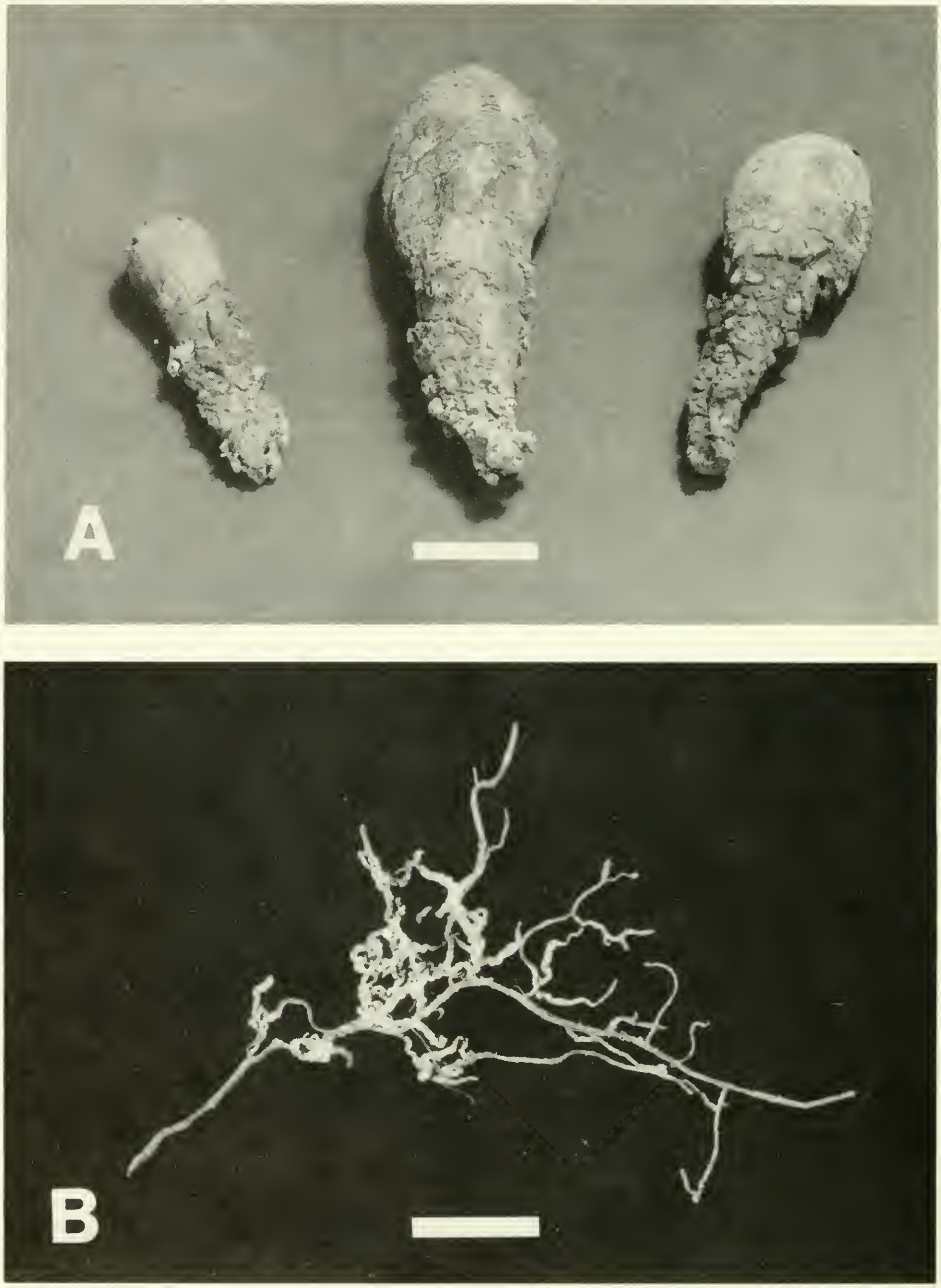

Fig. 1. *Pisolithus tinctorius* associated with California white fir on an eastern Sierra Nevada mine spoil: A, basidiocarps (bar represents 5 cm); B, ectomycorrhizae on roots (bar represents 1 cm).

description of those formed by *P. tinctorius* reported by Marx and Bryan (1975). Examination of the complete root system of an isolated white fir seedling with a single associated basidiocarp revealed numerous *P. tinctorius* ectomycorrhizae with approximately 35% of the roots exhibiting the bifurcate or coralloid form (Fig. 1B) or the fungal mantle characteristic of these mycorrhizae.

An earlier attempt to inoculate white fir seedlings at outplanting with *P. tinctorius* basidiospores was largely unsuccessful (Alvarez and Trappe 1983). The evidence presented here, however, indicates that this host and symbiont association occurs naturally in the Sierra Nevada. Efforts to monitor the mycorrhizal development of Sierra Nevada and Intermountain woody flora will continue in order to further ascertain the host ranges of this and other ectomycorrhizal fungi.

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BONE CHEWING BY ROCKY MOUNTAIN BIGHORN SHEEP

K. A. Keating[1]

Bone chewing has not, to my knowledge, been reported in wild North American bovids. Herein I describe an instance of bone chewing by a Rocky Mountain bighorn sheep (*Ovis canadensis*). An adult female consumed two bones on Mt. Evert's winter range in Yellowstone National Park during winter 1980–81. The bones apparently were from a small ungulate, probably bighorn sheep, mule deer, or pronghorn antelope. The first bone was consumed in 5–10 minutes; I interrupted consumption of the second. Sekulic and Estes (1977) report that sable antelope frequently spend ≤ 1 hr chewing a bone and described a case of a yearling male chewing on the same bone for 5.5 hr. The rapid consumption observed here was likely related to the weathered, brittle condition of the bones. Sekulic and Estes (1977) also report at least two instances in which bone possession by sable antelope led to aggressive displacement of younger animals by adult females. During my observations, several other bighorn sheep continued to feed nearby but showed no interest in the bone. Bone chewing was observed during the second of two unusually mild winters in which forage was generally free of snow and range use by elk was minimal. Indices of population quality are believed to reflect the nutritional status of a population (Geist 1971). In this study, high young:adult female ratios, long suckling times, male maturation rates, and low concentrations of lungworm (*Protostrongylus* spp.) larvae in bighorn feces were all indicative of a high-quality, expanding population (Keating 1982). This suggests that bone chewing was not a result of general nutritional deficiency in the population, though deficiencies in individual animals or in specific dietary components cannot be discounted.

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DISTRIBUTION OF LIMBER PINE DWARF MISTLETOE IN NEVADA

Robert L. Mathiasen[1] and Frank G. Hawksworth[2]

Limber pine dwarf mistletoe, *Arceuthobium cyanocarpum* (A. Nels. ex Rydb.) A. Nels. (Viscaceae), parasitizes several species of white pine (subgenus *Strobus*) in the western United States from Montana and Colorado to Oregon and California (Hawksworth and Wiens 1972, Mathiasen and Hawksworth 1988). The principal hosts of this mistletoe are limber pine (*Pinus flexilis* James), whitebark pine (*P. albicaulis* Engelm.), Great Basin bristlecone pine (*P. longaeva* D. K. Bailey), and Rocky Mountain bristlecone pine (*P. aristata* Engelm.). It also occurs on western white pine (*P. monticola* Dougl.) and foxtail pine (*P. balfouriana* Grev. & Balf.) in northern California (Hawksworth and Wiens 1972, Mathiasen and Hawksworth 1988). The limber pine dwarf mistletoe causes local, severe mortality in several areas (Hawksworth and Wiens 1972, Mathiasen and Hawksworth 1988).

The distribution of limber pine dwarf mistletoe in Nevada is poorly documented (Hawksworth and Wiens 1972, Hawksworth 1988, Kartez 1988). First collected in Nevada in 1881 on Great Basin bristlecone pine in the Spring Creek (Charleston) Mountains in Clark County, it was not collected elsewhere in Nevada until 1958 when it was found in the Ruby Mountains near Elko (Elko County) (Hawksworth and Wiens 1972). It has since been reported from the Sheep Mountains (Clark County), Copper and East Humboldt mountains (Elko County) (Hawksworth and Wiens 1984), and the South Snake Mountains (White Pine County) (collection by D. K. Bailey). Hawksworth (1988) suggests that the mistletoe probably occurred in the Toiyabe Mountains of Nye County because Linsdale et al. (1952) illustrated a limber pine that appeared to be infected by this mistletoe. This note confirms Hawksworth's suspicion that limber pine dwarf mistletoe occurs in the Toiyabe Mountains.

In 1989 the senior author found *Arceuthobium cyanocarpum* at several new localities in Nevada (Fig. 1): on limber pine in the North Snake Mountains (White Pine County) near Mount Moriah, in the Bull Run Mountains (Elko County) near Porter Peak, in the Santa Rosa Mountains (Humboldt County) south of Windy Gap, at three locations in the Toiyabe Mountains (North Toiyabe Peak and Bunker Hill, Lander County, and near Arc Dome, Nye County), and on the southeast slopes of Boundary Peak in the White Mountains (Esmeralda County) just east of the California state line. Limber pine dwarf mistletoe was also collected on limber pine and Great Basin bristlecone pine near Mount Washington in the South Snake Mountains, probably near the same location where D. K. Bailey collected it on Great Basin bristlecone pine. In addition, a population of limber pine dwarf mistletoe was found in the Warner Mountains of northeastern California (Modoc County) on whitebark pine. Specimens of dwarf mistletoes collected are deposited at the USDA Forest Service Pathology Herbarium (FPF), Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado. Four additional mountain ranges in Nevada were visited: the Toquima Mountains (Mount Jefferson area) and the Monitor Range (Monitor Peak area) in Lander County, the Independence Mountains (Jack Peak area) in Elko County, and the Pine Forest Mountains (Duffer Peak area) in Humboldt County. Although extensive populations of limber pine and/or whitebark pine were observed in those areas, no dwarf mistletoe was found. However, it is probable that the parasite occurs in other

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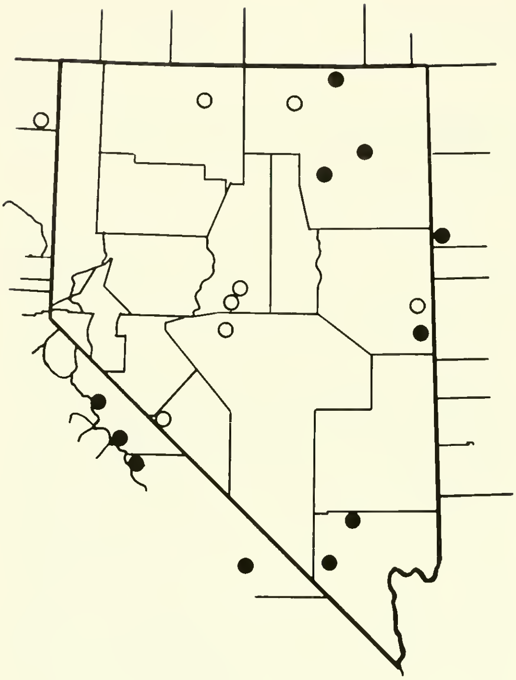

Fig. 1. Distribution of *Arceuthobium cyanocarpum* in Nevada and adjacent areas. Solid dots denote previously reported locations (Hawksworth and Wiens 1972, 1984), and open circles indicate locations first reported in this study.

parts of these ranges as well as other isolated mountain ranges in Nevada that support sizeable populations of limber pine, Great Basin bristlecone pine, or whitebark pine (Critchfield and Allenbaugh 1969, Critchfield and Little 1971).

Considering that limber pine dwarf mistletoe is noted for its extremely disjunct distribution in the western United States (Hawksworth and Wiens 1972, 1984) and its occurrence in adjacent areas in western Utah (Deep Creek Mountains) and eastern California (Panamint Mountains and Warner Mountains), it is not surprising to find it surviving in widely separated mountain ranges in Nevada. Both limber and Great Basin bristlecone pines occurred some 800 to 1,000 m lower than at present during the late Quaternary (Thompson and Mead 1982). Thus, their dwarf mistletoe was presumably much more widely distributed then also. However, as the climate warmed, the pines and their associated dwarf mistletoe receded to the higher elevations of major ranges and the dwarf mistletoe became restricted to scattered relictual populations.

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SOREX PREBLEI IN THE NORTHERN GREAT BASIN

Mark A. Ports[1] and Sarah B. George[2]

Sorex preblei has been described as a rare shrew of the Columbia basin, with a distribution extending as far east as the northwestern Great Plains (Junge and Hoffmann 1981). Its presence in the Great Basin desert is delineated by specimens that have been collected primarily on the periphery of this region (Zeveloff 1988). Other specimens have been collected from the northern, eastern, and western edges of the Great Basin. These include shrews from the northeastern corner of California (Williams 1984), the northwestern corner of Nevada (Hoffmann and Fisher 1978), eastern Oregon (Jackson 1922, 1928, Hansen 1964, Verts 1975), southeastern Washington (Armstrong 1957), west central Idaho (Larrison and Johnson 1981), Montana (Hoffmann et al. 1969, Hoffmann and Fisher 1978), western Wyoming (Hoffmann et al. 1969), and the south shore of the Great Salt Lake in Utah (Tomasi and Hoffmann 1984). There are no records from the Snake River Plain of southern Idaho or from the bulk of the Great Basin Desert in Nevada or Utah south of the 40th meridian.

Herein we report records of *Sorex preblei* from Elko County, Nevada, in the northern Great Basin. These records fill in a major gap in the distribution of the species and offer additional information on their habitat and sympatric associations with other species of *Sorex*.

The northern Great Basin is included in the Great Basin Division of the Intermountain Floristic Region (Holmgren 1972). This area includes the closed river basins of the Humboldt River and the Mary's River as well as the seasonally wet Bonneville Flats and the Snake River Plain. The region has a continental climate of fairly hot summers and cold, snowy winters. Approximately 130 fault-block mountain ranges following a north-to-northeast progression, and high valley floors are the prominent physiographic features. Within the higher valleys and river drainages are mesic to xeric shrublands dominated by *Artemisia* and *Chrysothamnus*. The river bottoms are dominated by more xeric halophytes such as *Sarcobatus* and *Chrysothamnus*.

Collection of *S. preblei* specimens from northern Elko County suggests that this shrew is more common and widespread in the northern Great Basin than previously supposed. A total of 12 specimens of *S. preblei* were collected near Sheep Creek, 10 km west of Haystack Ranch (55 km N of Elko); Sheep Creek drains the Independence Range. Seventy-five sunken pitfall traps were placed in a grid and shrews were sampled from this area from June to October 1984 (Ports and McAdoo 1986). Other *Sorex* include 31 *S. vagrans*, 13 *S. monticolus*, and 7 *S. merriami*. These specimens are housed at the Natural History Museum of Los Angeles and Northern Nevada Community College.

S. preblei was also collected approximately 49 km east of Sheep Creek in the perennial riparian willow and wild rose of the Mary's River. At this locality, approximately 87 km NE of Elko, a single specimen was taken in a snap trap on 12 June 1986. Also collected here were three specimens of *S. vagrans* and one specimen of *S. monticolus*.

These records fill in a distributional gap for *S. preblei* in the Great Basin. The only other record for this species in Nevada is from Washoe County (Hoffmann and Fisher 1978). To the east, *S. preblei* has been collected from the southern shore of the Great Salt Lake, Tooele Co., Utah (Tomasi and Hoffmann 1984). The specimen from the NW corner of Nevada, Washoe County, is approximately

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345 km from the Sheep Creek locality, whereas the Mary's River locality is approximately 233 km from the Great Salt Lake record. To the north, the nearest record of *S. preblei* is from the Jordan Valley, Malheur County, Oregon (Jackson 1922), approximately 223 km away from the north edge of the Great Basin. Both the Independence Range and the Mary's River are on the border of the floristic regions of the Great Basin to the south and the Columbia basin to the north (Holmgren 1972).

Some authors have suggested that *S. preblei* is found in marshy and riparian habitats (Larrison and Johnson 1981), whereas others have stated that this species prefers "arid to semiarid shrub-grass associations or openings in montane coniferous forest dominated by sagebrush" (Tomasi and Hoffmann 1984). Our habitat observations in northeastern Nevada only partially agree with those of Tomasi and Hoffmann (1984).

At the Sheep Creek locality we collected *S. preblei* in a seasonally wet, sagebrush-dominated community. The stream exhibits a snowmelt spring runoff from early spring until early summer, and then it dries up. Big sagebrush (*Artemisia tridentata*), rubber rabbitbrush (*Chrysothamnus nauseosus*), and antelope bitterbrush (*Purshia tridentata*) provide a dense overstory, and a variety of bunchgrass species and forbs provide a stable understory. By the end of summer, the grasses and forbs have seeded and the area is very dry. The elevation at this locality is 2,150 m. The Mary's River locality has a perennial source of water from the Jarbidge Mountains to the north. The soils here tend to be more fertile with extensive meadows, and the dominant vegetation includes willows (*Salix* sp.), Wood's rose (*Rosa woodsii*), greasewood (*Sarcobatus* sp.), and Great Basin wildrye (*Elymus canadensis*). Other grasses and forbs provide an abundant cover in adjacent meadows that are cut seasonally for hay.

Williams (1984) has collected *S. preblei* in similar mixed sagebrush, aspen, and willow riparian habitats in the Warner Mountains of northeastern California.

Six years of shrew trapping by the senior author in wet meadows, montane coniferous forest, and high-elevation mountain brush of northeastern and central Nevada have failed to turn up a specimen of *S. preblei* (Ports and McAdoo 1986). The most likely habitat associations for *S. preblei* in this area seem to be ephemeral and perennial streams dominated by shrubs, primarily below 2,500 m in elevation.

Although sympatry among species of long-tailed shrews is common in the western United States (Spencer and Pettus 1966, Williams 1984), *S. preblei* has rarely been captured in association with other shrews. Junge and Hoffmann (1981) found *S. preblei* associated with its congener, *S. cinereus haydeni*, in coniferous forest–mountain shrub habitats in Yellowstone County, Montana. In California's Warner Mountains, *S. preblei* is sympatric with *S. vagrans* and *S. merriami* in ecotonal habitats of forested riparian and dry shrublands (Williams 1984).

Herein we document the association of *S. preblei* with three other species of *Sorex*. It is difficult to explain why the plant community at Sheep Creek, which is a xeric, ephemeral stream habitat, can support four species of shrews, whereas the more mesic, complex mountain habitat in the Warner Mountains and the perennial riparian habitat on the Mary's River support only three shrew species. Certainly it is unusual to find *S. monticolus* in a low-elevation, sagebrush community; this species is normally associated with more mesic habitats in Nevada (Hall 1946).

Churchfield (in press) suggests that shrews are very flexible in their foraging habits and will decrease their dietary overlap when the number of shrew species in a community increases. Dietary generalists usually are found in greater numbers than dietary specialists in multi-species communities. This may be the case with shrew communities in the Great Basin, but these species assemblages will be explained only with detailed ecological studies examining microhabitats, diets, and life-history patterns, plus comprehensive trapping to insure that all shrew species in a particular area are well documented.

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MAYFLY GROWTH AND POPULATION DENSITY IN CONSTANT AND VARIABLE TEMPERATURE REGIMES

Russell B. Rader[1,2] and James V. Ward[1]

ABSTRACT.—The thermal equilibrium hypothesis predicts that aquatic insect body size/fecundity and, consequently, population density and biomass will be maximized in geographic areas or along altitudinal gradients where the thermal regime is optimal with respect to growth and development. Seasonal growth analyses of three mayfly species, combined with detailed thermal descriptions, were used to explore differences in body size and fecundity at three sites with similar elevations but different temperature regimes. Site 1 was located near the upper altitudinal distribution for each species, whereas sites 2 and 3 were located below a deep-release storage reservoir. The temperature pattern at site 1 had rapid seasonal changes, with a short summer and a long, freezing winter. Site 2 demonstrated gradual seasonal changes combined with winter warm and summer cool temperatures. Site 3 was intermediate with respect to seasonal change and winter harshness but had the highest maximum and mean annual temperatures. Mayfly development at site 1 was characterized by slow growth during the summer-autumn period, no growth during the winter, and a rapid increase during the spring-summer period. In contrast, growth at site 2 was continuous throughout the year, including the winter. Growth at site 3 was either continuous across sites or rapid during the spring-summer period, depending on the species. Based upon the interactions among temperature, body size, and metabolic costs, the thermal equilibrium hypothesis was successful at predicting body size and fecundity differences among sites. It was less successful at predicting variation in population density and biomass. Density-dependent and density-independent sources of mortality, including temperature, may interrupt the translation of higher fecundity into higher population density and biomass.

Temperature, because of its influence on metabolism, growth, and reproductive success, is a dominant ecological determinant of the geographical and altitudinal distributions of aquatic insects (e.g., Vannote and Sweeney 1980, Ward and Stanford 1982, Sweeney 1984, Ward 1986). The thermal equilibrium hypothesis (TE) is a conceptual model of the effects of temperature on aquatic insect metabolism, growth, body size, and therefore fecundity (Sweeney and Vannote 1978, Vannote and Sweeney 1980). It predicts that population density, distribution, and stability (Connell and Sousa 1983) are determined by individual reproductive success and will be maximized in geographic areas or along altitudinal gradients where the thermal regime is optimal with respect to growth, development, and body size. Fecundity, an essential component, but not the only factor defining reproductive success, should decrease in temperature regimes warmer or cooler than optimal. Other factors, which may influence fecundity and may or may not be influenced by temperature, can determine population size and distribution (e.g., egg-hatching success, emergence success, mating success, feeding rates, assimilation efficiency, food quality and quantity, biotic interactions). The TE hypothesis, however, attempts to define the influence of temperature on population size and distribution based only on the effect of temperature on metabolism, growth, and therefore body size/fecundity.

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The objective of this study was to analyze the influence of temperature on the growth and body size/fecundity of three mayfly species and compare these results with population size (density and biomass) data and the predictions of the thermal equilibrium hypothesis. Three sites were chosen on the same river, all with similar elevations but different temperature regimes. Site 1 was located near the upper altitudinal limit for each species, whereas sites 2 and 3 were located in a warmer, more constant thermal regime downstream from a deep-release reservoir. Specifically, we sought to test the following hypotheses: (1) population size and body size will be smaller for each species at site 1 compared with sites 2 and 3; (2) population size will correspond with body size at the same sites (i.e., site-specific ranks of body size and population size should be the same); (3) seasonal patterns of growth will parallel seasonal temperature patterns. Body size/fecundity was compared to examine its ability to explain among-site differences in population size.

Several studies have demonstrated a positive correlation between body size and fecundity in aquatic insects (see Clifford and Boerger 1974, Kondratieff and Voshell 1980, Sweeney and Vannote 1981). Therefore, we assume that larger mayflies produce more eggs compared with smaller mayflies of the same species. We did not attempt to determine, as predicted by the TE hypothesis and numerous other authors, whether an increase in population size is positively correlated with an increase in population stability. Considerable evidence, however, indicates that larger populations are more stable than smaller populations (e.g., smaller populations are more susceptible to extinction).

STUDY SITES AND INSECT ALTITUDINAL DISTRIBUTIONS

The first hypothesis required us to a priori rank the study sites according to how closely they approximated the optimal temperature conditions for the mayflies under investigation. Our ranks were based on the altitudinal distributions of the insects. Because the study sites were located near their upper limits, the unaltered temperature regime at site 1 was considered cooler than the optimum necessary to maximize body size/fecundity. Therefore, the warmer, dam-impacted sites 2 and 3 were assumed to be nearer the insects' optimal temperature regime. There was no a priori reason to separate sites 2 and 3 with respect to their influence on growth, body size, and population size even though they had very different temperature regimes.

The study was conducted in the Upper Colorado River on the western slope of the Rocky Mountains in the vicinity of Granby Reservoir, a large (666 km^3), deep-release storage impoundment. Granby Reservoir is located 38 km northwest of Denver, Colorado. Site 1 was located in a third-order, free-flowing section of the river 4.0 km above the reservoir; sites 2 and 3 were located 0.4 and 4.0 km, respectively, downstream from the dam. Although differentially influenced by stream regulation, all three sites had similar gradients (0.006–0.009), canopy cover, geology, riparian vegetation, and elevation (2,593 m, 2,454 m, and 2,426 m, respectively. (For complete site descriptions see Rader and Ward [1988].)

Three mayfly species were analyzed in this study: *Drunella grandis* (Eaton), *Ephemerella infrequens* (McDunnough), and *Baetis tricaudatus* (Dodds). Ward (1980, 1986) determined the altitudinal distribution of macroinvertebrates, including the mayflies of this study, in the St. Vrain River, a free-flowing stream running from the alpine tundra to the plains on the eastern slope of the Rocky Mountains. Based on his results, site 1 of this study (upper montane zone) was above the altitudinal distribution for *D. grandis* and very near the upper limits for *E. infrequens* and *B. tricaudatus*. All three species exhibited maximum densities at lower elevations in the foothills or plains zones. Even though their altitudinal upper limits appear to be somewhat higher in the Colorado River, probably because of its larger size compared with the St. Vrain River, we concluded that all three study sites were located near the upper altitudinal limit for each of the three mayfly species.

METHODS

Temperature, Growth, and Body Size

Water temperature was measured continuously at each site for 18 months using Ryan 90-day thermographs. Each thermograph was checked against a Weksler hand-held thermometer on a monthly basis and calibrated prior to placement and following retrieval. Daily mean temperatures were used to calculate annual mean temperatures, annual coefficient of variation, annual degree days, number of days less than 3 C, number of days equal to 0 C, length of spring-summer and summer-autumn periods, and rate of spring-summer increase and summer-autumn decline.

Annual growth rate analyses and general temperature descriptors (e.g., accumulated degree days, mean annual temperature, etc.) cannot explain site-specific variation in aquatic insect body size and fecundity because they average over important seasonal information. Seasonal growth rate analyses combined with seasonal temperature profiles can, however, provide insights into the relationships between temperature, growth, and body size.

Temperature profiles for each site were separated into three periods: (1) spring-summer, (2) summer-autumn, and (3) winter (Fig. 1). The winter period was defined by mean daily temperatures <3 C in order to include the winter warm temperatures at site 2. The end of the spring-summer period/beginning of the summer-autumn period was set at 15 August, based on temperature peaks apparent at sites 1 and 3 (Fig. 1). Therefore, the spring-summer period began when the mean daily temperature exceeded 3 C and ended 15 August. The summer-autumn period began 15 August and ended when the mean daily temperature dropped below 3 C.

Growth, defined as the monthly increase in mean biomass of individuals collected per sampling date, was determined for *D. grandis* and *E. infrequens*. Growth for *B. tricaudatus* was not analyzed because of difficulty in assigning intermediate-sized instars to the correct generation.

Site-specific differences in seasonal growth rates were determined by regressing monthly mean individual biomass estimates against the number of Julian days accumulated over the three separate growth periods (spring-summer, summer-autumn, and winter). A slopes comparison test (analysis of covariance) was used to determine among-site differences in seasonal growth rates. No transformation was necessary because growth was linear over the short seasonal periods.

Population Size and Body Size

Estimates of population density and biomass were based on four Surber samples (0.09^2m each, 240 µm mesh) collected monthly across the width of the stream at each site and four artificial substrates. Artificial substrates consisted of clay bricks (23 × 19 × 9.5 cm) that had been in the streams for one month before being sampled. Most of the Surber samples enclosed natural substrate particles similar in size to the artificial brick substrates. Therefore, sampling units from both techniques were combined because the sampling areas were approximately equal. A simple *t* test indicated that the mayfly population means based on Surber samples of natural substrate were not significantly ($P = .63$) different from population means based on the artificial substrate samples. Following identification and enumeration, all nymphs were divided into 0.1-mm size classes, based on maximum head capsule width, and dried at 60 C for 48 hours. Mean annual population biomass was determined by summing biomass estimates for all size classes across all sampling dates. Mean annual population density was determined after summing the number of individuals in each size class at each site. Head-capsule measurements were also used to construct size-frequency plots for life-history determinations, including the number of annual generations produced. Complete life-history information for these species at each site can be found in Rader and Ward (1989).

Female body size (dry weight biomass) of late instars was estimated by taking the mean of the three largest size classes collected from each site. Late mayfly instars have a full complement of mature eggs.

RESULTS

Temperature, Growth, and Body Size

A progressive increase in accumulated degree days and mean annual temperatures was found from site 1 to site 3 (Table 1). Site 1 was characterized by rapid seasonal changes in temperature and a long, freezing (0 C) winter (Table 1, Fig. 1). In contrast, site 2 demonstrated gradual seasonal changes combined with winter warm and summer cool temperatures. Site 3 was intermediate with respect to rates of seasonal change but had the greatest amount of thermal energy (largest number of accumulated degree days, largest maximum temperature, and largest annual mean temperature).

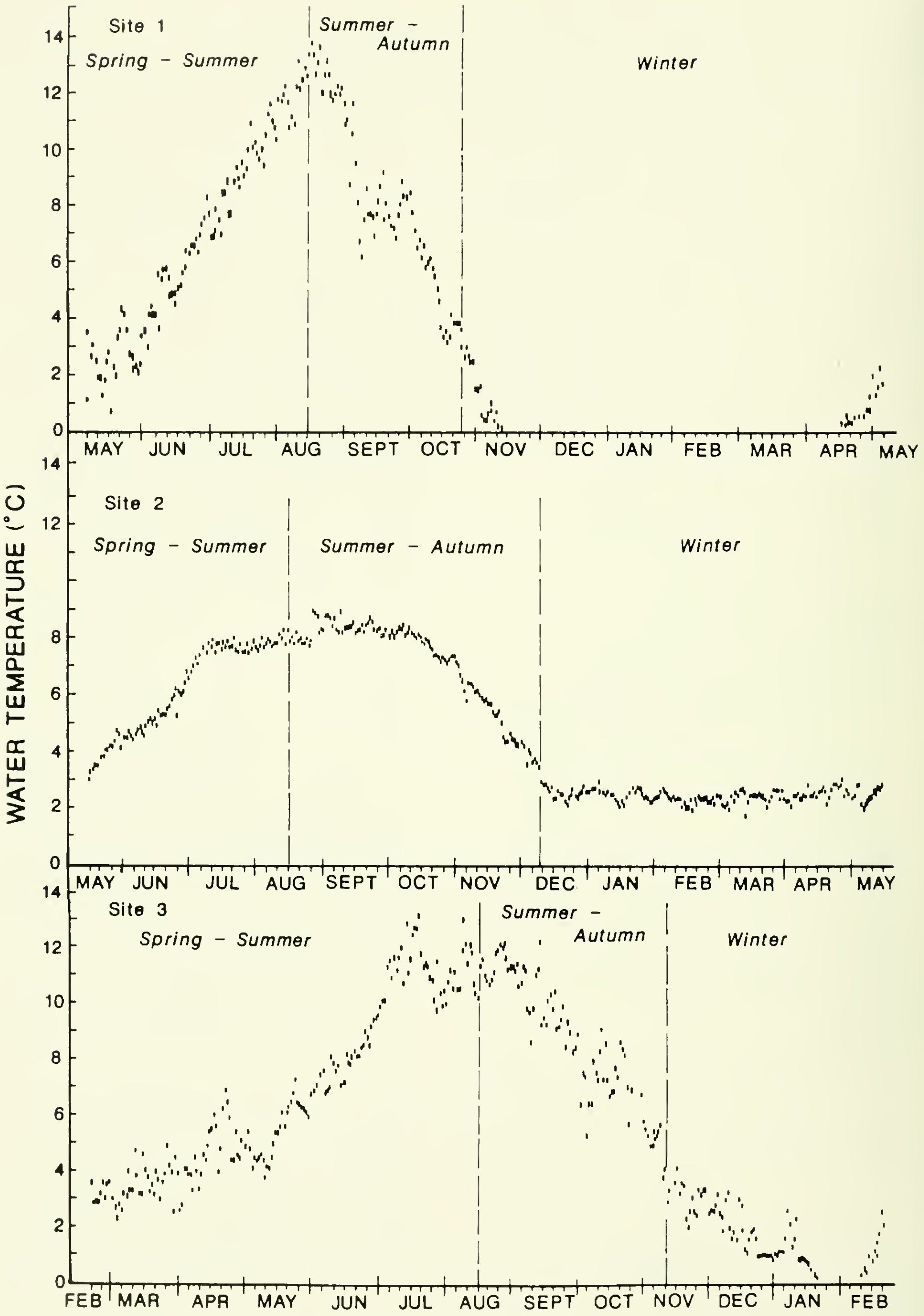

Fig. 1. Temperature profiles for each site during 1981–1982. Individual points represent daily means. (See text for explanation of criteria used to determine seasonal separations. Note that the x-axes have been adjusted to facilitate a comparison of the length of each period at each site.)

TABLE 1. Temperature characteristics of each site.

Characteristic	Site 1	Site 2	Site 3
Annual degree days (C)	1130	1729	2082
Mean annual temperature (C)	3.6	4.7	5.7
C.V. (%)	119	53	64
Minimum (C)	0.0	1.8	0.0
Maximum (C)	18.0	9.8	18.2
Days <3 C	191	155	101
Days = 0 C	153	0	17
Rate of spring-summer ↑ (°C/day)	0.14	0.05	0.06
Length of spring-summer (days)	99	94	177
Rate of summer-autumn ↓ (°C/day)	0.20	0.05	0.10
Length of summer-autumn (days)	70	115	87

Seasonal growth rates were analyzed to explain among-site differences in body size for each species. The seasonal pattern of growth for *D. grandis* and *E. infrequens* at site 1 was characterized by slow growth during summer-autumn, no growth during winter, and a rapid increase during the spring-summer period (Figs. 2, 3). In contrast, growth at site 2 was comparatively fast and continuous through each seasonal period including winter. At site 3, *D. grandis* demonstrated a continuous growth pattern similar to that observed at site 2, whereas *E. infrequens* demonstrated a spring-summer pulsed pattern of growth more similar to that at site 1.

The seasonal growth rate (0.0108 mg/day) for the early instars of *E. infrequens* during the summer-autumn period was significantly ($P = .0001$) faster at site 2 than at sites 1 and 3 (0.004 and 0.003 mg/day, respectively), which were not significantly different (Fig. 2). This trend continued into the winter period when the growth rate at site 2 (0.022 mg/day) was again significantly ($P = .0001$) faster than at sites 1 and 3, where growth rate was not different from zero. By the end of winter, the site 2 population had completed over 76% of its growth, and larvae were over five times larger than those at sites 1 and 3 (Fig. 2). Therefore, the larger body sizes at site 2 can be attributed to rapid growth starting at egg hatch and continuing through the winter. During the spring-summer growth period, individuals at sites 1 and 3 grew significantly ($P = .0001$) faster (0.034 and 0.033 mg/day, respectively) than individuals at site 2 (0.014 mg/day). However, the body sizes of late instar larvae at sites 1 and 3 were still considerably smaller than those at site 2.

The growth rate (0.064 mg/day) of early instars of *D. grandis* during the summer-autumn period was significantly different among sites ($P = .0001$), being greatest at site 2 and slowest at site 1 (0.035 mg/day). Winter growth was also faster at site 2, with an average rate of 0.064 mg/day, followed by site 3 (0.044 mg/day) and then site 1 (0.015 mg/day). Winter growth at site 1 was not significantly different from zero. Spring-summer growth at site 1, however, was significantly ($P = .0001$) faster than at sites 2 or 3, with the fastest seasonal rate of increase for this study (0.119 mg/day). Spring-summer growth rates at sites 2 and 3 (0.076 and 0.055 mg/day, respectively) were not significantly different.

Baetis tricaudatus was univoltine at site 1, but bivoltine with slow and fast seasonal generations at sites 2 and 3. In contrast, *D. grandis* and *E. infrequens* had univoltine, slow seasonal life cycles at each site. Complete life-history data for each species can be found in Rader and Ward (1989).

As predicted by the first hypothesis, mean annual density and biomass of each species were much greater at the warmer sites below the dam than at site 1 (Table 2). Population density and biomass of *Baetis tricaudatus* and *E. infrequens* were largest at site 2, followed by sites 3 and 1. Maximum density and biomass of *D. grandis* were greatest at site 3, followed by sites 2 and 1.

Contrary to the predictions of the second hypothesis, dry weights of the largest instars, and population sizes of each species, did not correspond when ranked by sites (Table 2). Although the largest late instars of *E. infrequens* occurred at site 2, where the density was greatest, the largest instars of *B. tricaudatus* and *D. grandis* did not occur in the largest population. Body size and population size corresponded in only two other instances; the smallest late instars of *B. tricaudatus* and the intermediate-sized late instars of *D. grandis* occurred in the small- and intermediate-sized populations, respectively, at site 1.

The largest *B. tricaudatus* larvae occurred at site 3, whereas its maximum population density and biomass occurred at site 2. Late *B. tricaudatus* instars at sites 2 and 3 were over two times larger than late instars at site 1 (Table 2). The largest-sized larvae of *D. grandis* occurred at site 2. Site 3, which had the largest population of *D. grandis*, had the smallest late instars (Table 2).

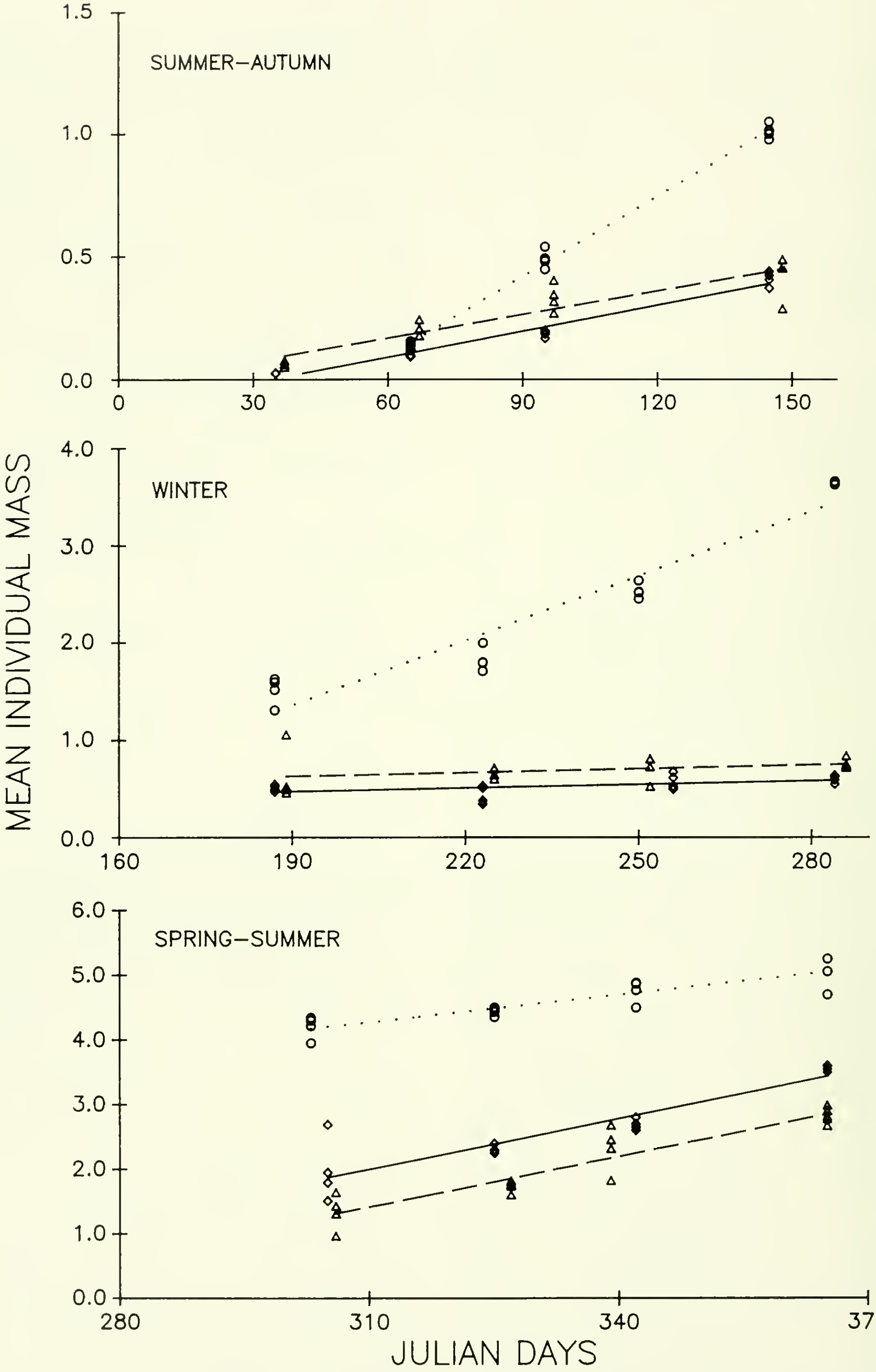

Fig. 2. Seasonal growth rate patterns for *Ephemerella infrequens*. Site 1 is represented by a solid line and diamonds, sites 2 and 3 by a dotted line and circles, and a dashed line and triangles, respectively. Each symbol (diamond, circle, and triangle) represents the mean biomass for a single sample.

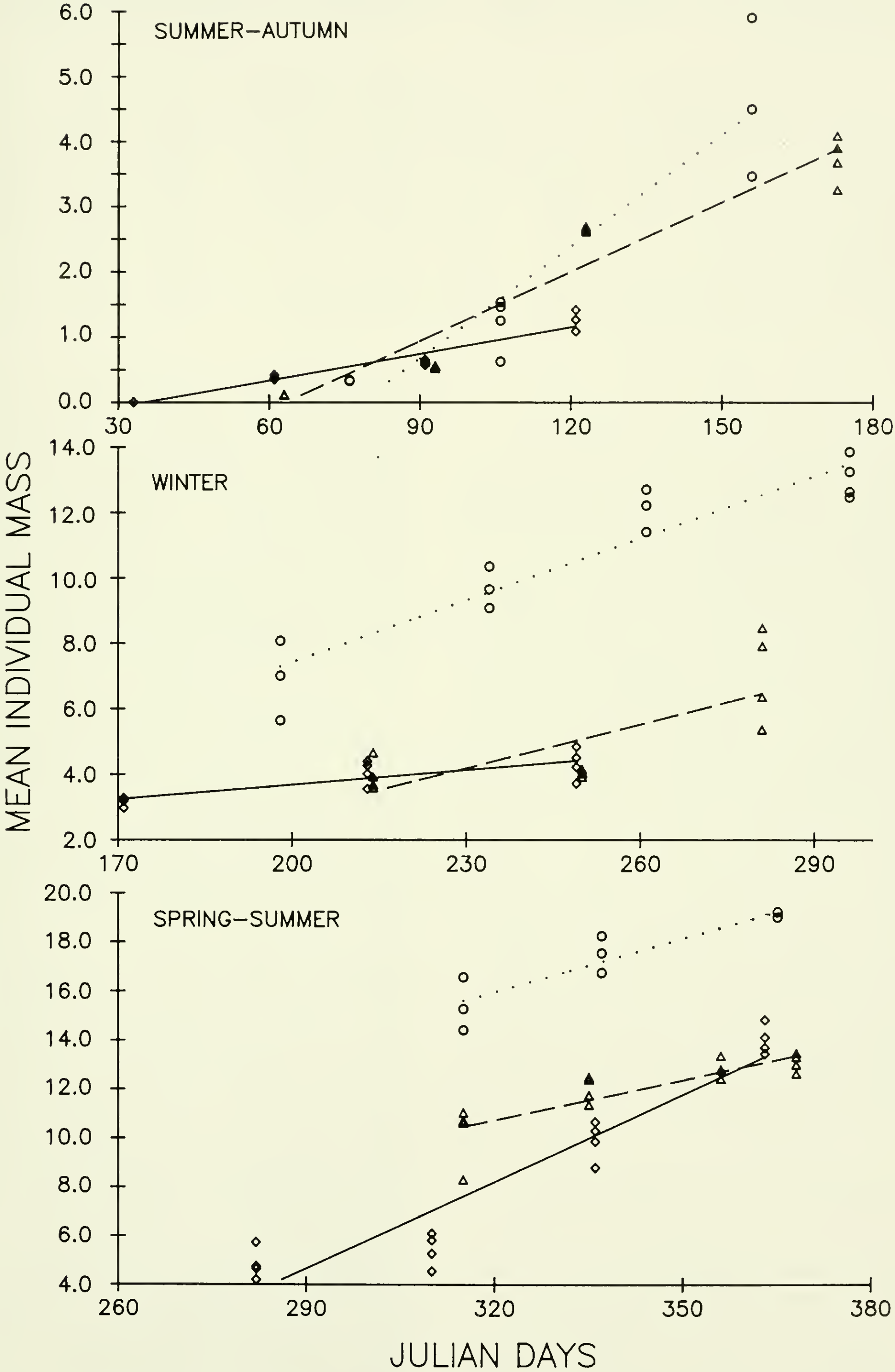

Fig. 3. Seasonal growth rate patterns for *Drunella grandis*. (For further description, see Fig. 2 legend.)

Table 2. Mean annual population density (#'s m^{-2}) and biomass (mg m^{-2}), plus mean individual size (mg dry wt.) for late instars of each species. Values in parentheses for the population parameters are the percentage of mean represented by the standard error. Values in parentheses for size estimates indicate the number of individuals used to determine each mean.

	Site 1			Site 2			Site 3		
	Population size		Body size	Population size		Body size	Population size		Body size
Species	Density	Biomass		Density	Biomass		Density	Biomass	
B. tricaudatus	754	142.6	0.730	7720	1501.7	0.550	4018	1162.8	1.960
	(21%)	(17%)	(31)	(18%)	(21%)	(35)	(18%)	(27%)	(35)
E. infrequens	367	502.6	3.500	1034	4964.7	4.930	644	1188.5	2.800
	(25%)	(23%)	(23)	(23%)	(25%)	(35)	(24%)	(26%)	(25)
D. grandis	102	1585.9	14.930	80	2368.4	18.110	278	3355.4	14.220
	(31%)	(18%)	(16)	(10%)	(22%)	(9)	(14%)	(20%)	(17)

Discussion

Temperature, Growth, and Body Size

The winter warm and summer cool conditions of site 2 allowed rapid continuous growth of *E. infrequens* and *D. grandis*, which produced larger instars and greater fecundity. Site-specific explanations of growth patterns and body-size differences for *D. grandis* and *E. infrequens* are consistent with the TE hypothesis. Vannote and Sweeney (1980) proposed that the seasonal pattern of growth for aquatic insects, as for other small ectotherms (e.g., Phillipson 1981), may be determined by the interaction between temperature and body size. Smaller instars, which have a large surface-to-volume ratio, will have a higher metabolic rate than larger instars at the same temperature. At site 1 the smallest *D. grandis* and *E. infrequens* instars appeared during the warmest months of the year (July, August, and September). High summer-autumn temperatures coincident with small instars at site 1 likely resulted in large metabolic costs and, therefore, slow growth rates and possibly high mortality rates. Both species ceased to grow during the freezing winter temperatures. In the spring, winter survivors experienced a rapid increase in temperature and thus a relatively short period (99 days or less) to complete growth and maturation. All else being equal, the magnitude and length of summer-autumn temperatures when coincident with early instars, plus the rate of vernal rise, limit growth and body size/fecundity and probably have an important influence on the geographic distribution and upper altitudinal limits of aquatic insects. This may be especially applicable to cool-adapted boreal species (see Edmunds 1982).

Early instars at site 2 began growth in much cooler summer-autumn temperatures; metabolic costs were low and growth rates fast compared to those at sites 1 and 3. Winter temperatures, which varied slightly around 2 C, were not sufficiently cold to inhibit growth, which continued at a rapid pace. Growth appeared near completion before the vernal rise in temperature, thus leaving plenty of time for maturation and emergence. The rapid completion of growth probably resulted in the extended emergence of *E. infrequens* and the addition of a second generation of *B. tricaudatus* at site 2.

The early instars of *D. grandis* (July) and *E. infrequens* (August and September) began growth at site 3 during the warmest months of the year. August and September were, on average, 7–8 C warmer at site 3 than site 2. Although *E. infrequens* did not grow, *D. grandis* early instars grew rapidly during the summer-autumn growth period. Because *D. grandis* early instars were approximately two times larger than *E. infrequens* early instars, they probably had lower metabolic costs. This allowed them to grow at the warm summer-autumn temperatures. Although both species stopped growing during winter at site 1 but continued to grow during winter at site 2, only *D. grandis* continued winter growth at site 3. The fact that *D. grandis* was over three times larger than *E. infrequens* at the beginning of winter may explain its ability to grow in winter at site 3 in contrast to *E. infrequens*.

These site-specific explanations of growth are consistent with the TE hypothesis suggesting that growth rate and consequently body size and fecundity are determined by the length of time individuals are exposed to a specific optimal range of temperatures. Other factors, however, that may also influence mayfly growth rates (e.g., food abundance; Sweeney et al. 1986) were altered by the effects of stream regulation. For example, constant flow conditions and the addition of planktonic diatoms from the reservoir enhanced food quality and quantity at sites 2 and 3 (Rader and Ward 1989).

If summer temperatures increase metabolic costs, causing growth to slow or stop, then the rate of vernal rise and autumn decline determines the amount of time individuals are exposed to optimal temperatures and, therefore, the amount of time available for growth. Growth of both *D. grandis* and *E. infrequens* continued as long as temperatures remained between 2 C and 10 C. However, when temperatures exceeded this range, growth slowed or stopped. Where growth was continuous (site 2), temperatures were always within this range. The optimal temperature range for these two species appears to lie between 2 C and 10 C.

Population Size and Body Size

Winter warm and summer cool conditions at site 2 and the long spring-summer period at site 3 probably accounted for the multivoltine life cycle of *B. tricaudatus* at these sites. Stanley and Short (1988) suggested that population size may remain unaltered or even increase in warmer than optimal conditions if faster growth rates and shorter generation times compensate for smaller body sizes and lower fecundity. For some aquatic insects, warmer than optimal temperatures may offer a tradeoff between body size/fecundity and generation time. Will they maximize reproductive effort by producing fewer, larger individuals (slow growth and a univoltine life cycle) or many, smaller individuals (fast growth and multivoltine life cycle)? These data demonstrated that *Baetis* may have the genetic plasticity necessary to respond to such tradeoffs. As temperatures approached optimality (site 2) from cooler conditions (site 1), both voltinism and body size increased within the same population. When comparing site 1 with the much warmer and very different temperature regimes downstream from the reservoir, we found that our data support the predictions of the TE hypothesis. The largest body size and population size of each species occurred downstream from the reservoir. However, site-specific comparisons of body size and population size did not correspond as predicted by the TE hypothesis. The thermal regimes at sites 2 and 3 were apparently sufficiently similar that temperature did not have an overriding influence on population sizes. The TE hypothesis assumes that higher fecundity is equivalent to larger population size. Sources of mortality at every stage of development, eggs, nymphs, and adults (Sweeney and Vannote 1982, Butler 1984, Peckarsky 1984, Gilliam et al. 1989), which may vary across sites, may interrupt the translation of higher fecundity into higher population density and biomass. Numerous factors, in addition to the influence of temperature on body size/fecundity, will undoubtedly influence the geographic or altitudinal variation in aquatic insect population size and stability. Toward the center, and probably over most of a species range, other sources of mortality and determinants of reproductive success should have a greater influence on aquatic insect population size. Temperature at the edge of a species range may, however, be more limiting, compared to other factors, in determining the extent of a species distribution.

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BLACK-TAILED PRAIRIE DOG POPULATIONS ONE YEAR AFTER TREATMENT WITH RODENTICIDES

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ABSTRACT.—Three rodenticide treatments, zinc phosphide with prebait, strychnine with prebait, and strychnine without prebait, were applied to black-tailed prairie dog (*Cynomys ludovicianus*) colonies in west central South Dakota. Results were compared immediately posttreatment and for one year after application. Zinc phosphide was the most effective for reducing prairie dog numbers immediately. When burrow activity levels of prairie dogs were initially reduced by 45% with strychnine only, they returned to untreated levels within ten months. When initial reductions were 95% with zinc phosphide, however, the number of active burrows was still reduced 77% in September the following year. Strychnine with prebait treatment showed initial reductions of 83% in burrow activity. Bait consumption by prairie dogs was highest for zinc phosphide.

Rodenticide-treated oats have been and are the primary tool for control of black-tailed prairie dogs (*Cynomys ludovicianus*) to prevent expansion of colonies on the plains. Widespread control programs for prairie dogs have been common on the Great Plains for over 100 years (Merriam 1902) and are still common practices (Schenbeck 1982). Strychnine, first introduced into the United States about 1847, has had varied success as a rodenticide (Crabtree 1962). The alkaloid form on grain was recommended by the U.S. Department of Agriculture at the beginning of the century. Two characteristics that may have impeded its acceptance by rodents are its bitter taste and the noxious effect of sublethal doses; attempts to circumvent these characteristics have failed. Strychnine also is considered hazardous to many nontarget species (Tietjen 1976a).

Zinc phosphide was introduced as a vertebrate pest-control agent in 1943 because of strychnine shortages during World War II (Crabtree 1962). However, use of zinc phosphide as a field rodenticide was limited until 1976, when it was developed specifically for black-tailed prairie dog control (Tietjen 1976a). Since then, zinc phosphide has been the only rodenticide federally approved for prairie dog control. Bioassays have shown that zinc phosphide causes no secondary poisoning of predatory or scavenging wildlife (Crabtree 1962, Tietjen 1976a).

The objectives of this study were to determine (1) seasonal activity of prairie dogs and (2) short- and long-term effects of zinc phosphide (with prebait), strychnine with prebait, and strychnine without prebait on prairie dog colonies during the one-year period following rodenticide application. Immediate effects of the three rodenticide treatments have been reported by Uresk et al. (1986).

STUDY AREA

The study was conducted in Badlands National Park and Buffalo Gap National Grassland in west central South Dakota. The climate is considered semiarid, with a 12-year average annual precipitation of 40 cm at the Cedar Pass Visitors Center, Badlands National Park. Approximately 80% of the total precipitation falls as thundershowers from April to September. Temperatures range from −5 C in January to 43 C in July, with an average annual temperature of 10 C.

Raymond and King (1976) described the soils on the study area as sedimentary deposits of clay, silt, gravel, and volcanic ash. Topographic features consist of rugged pinnacles, vegetated tabletop buttes, creek gullies, and grassland basins. Gently rolling grasslands in the northern portion of the study area ranged from 700 to 1,000 m in elevation.

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The vegetation comprises a mosaic of native grasses, forbs, shrubs, and isolated trees. Dominant grasses include blue grama (*Bouteloua gracilis*), buffalograss (*Buchloe dactyloides*), needleleaf sedge (*Carex eleocharis*), and western wheatgrass (*Agropyron smithii*) (Uresk 1984). Common forbs include scarlet mallow (*Sphaeralcea coccinea*), American vetch (*Vicia americana*), dogweed (*Dyssodia papposa*), sage (*Salvia reflexa*), and prairie sunflower (*Helianthus petiolaris*). The dominant shrub is pasture sagebrush (*Artemisia frigida*), and nonnative grasses include cheatgrass (*Bromus tectorum*) and Japanese chess (*B. japonicus*).

Native herbivores inhabiting the Badlands region are the black-tailed prairie dog, mule deer (*Odocoileus hemionus*), Rocky Mountain bighorn sheep (*Ovis canadensis*), American bison (*Bison bison*), pronghorn (*Antilocapra americana*), black-tailed jackrabbit (*Lepus californicus*), white-tailed jackrabbit (*L. townsendii*), and eastern cottontail (*Sylvilagus floridanus*). Small rodents include the deer mouse (*Peromyscus maniculatus*) and grasshopper mouse (*Onychomys leucogaster*). Livestock are not present in the Park, but bison graze the area all year. Cattle are allowed to graze on the National Grassland for six months during the growing season each year.

METHODS

Eighteen sites on 15 prairie dog colonies were sampled in 1983 and 1984, with 9 designated as treatments sites and 9 as controls (Uresk et al. 1986). Sites were clustered into three major areas, one for each rodenticide treatment, containing three treatment and three control sites. Zinc phosphide was applied to the area within Badlands National Park because administrative restraints forbid the use of strychnine: four sites were clustered and paired on an approximately 600-ha prairie dog colony. The other two sites were located on prairie dog colonies northwest of the larger colony and northeast on a colony in the Buffalo Gap National Grassland. The other two treatments, strychnine with and without prebait, were randomly assigned to the two remaining major areas on the National Grassland. All treated and control sites were randomly assigned in the clusters. The area with prebaited strychnine was located in Conata Basin, and the area treated with strychnine only was located east and south of Scenic. All treatment and control sites were on isolated towns ranging from 12 to 283 ha. Within each treatment regime, treatment or control designation was assigned randomly except where administrative restrictions applied.

The open-burrow technique used to determine the effectiveness of the rodenticide treatments evaluated the number of active burrows (Tietjen and Matschke 1982). Burrow entrances in a 100 × 100-m area (1-ha) were filled (plugged) with soil to prevent egress/ingress by prairie dogs. Forty-eight hours later the reopened burrows large enough for prairie dogs to pass through were counted. Burrow activity for pretreatment periods was recorded in June, July, and early September 1983. Posttreatment counts were taken in late September 1983 (four days after poisoning) and in June, July, August, and early September 1984.

Treated and untreated steam-rolled oats were obtained from the U.S. Fish and Wildlife Service (USFWS), Pocatello Idaho Supply Depot. Poisons were applied in the field, in accordance with federal label instructions, when proper environmental conditions existed to insure optimum consumption of oats by prairie dogs (Tietjen 1976a, 1976b, Tietjen and Matschke 1982). Untreated oats (prebait) and the poisoned oats were applied on large areas from 3-wheel-drive, all-terrain cycles fitted with bait dispensers (Schenbeck 1982), and by hand with teaspoons on smaller areas.

At the six sites requiring prebaiting, 4 g of high-quality, untreated steam-rolled oats was applied as prebait at a minimum of 95% of the burrows. Three sites were prebaited on 20 and 21 September 1983. Prebait was applied (<0.01-m^2 area) at the edges of prairie dog mounds.

Prebaited areas were examined before poisoned oat treatment to assure that the prebait was consumed by prairie dogs. Three days after prebait application (22 September 1983), three sites were treated with 4 g of 2.0% active zinc phosphide steam-rolled oats. Three additional sites were treated with 8 g of 0.5% strychnine alkaloid steam-rolled oats per burrow on 23 September 1983. The last three

TABLE 1. Average number of black-tailed prairie dog burrows/ha, active burrows/ha, and percent active burrows/ha (± standard error of the mean) on untreated areas for four sampling periods in 1983 and 1984 in west central South Dakota.

Sampling period	Total burrows/ha	Number active/ha	Percent active
1983			
June[a]	121 ± 9	98 ± 8	81 ± 3
July[a]	117 ± 9	87 ± 8	74 ± 3
Early September[a]	113 ± 8	48 ± 5	43 ± 3
Late September[b]	104 ± 13	34 ± 4	35 ± 4
1984[b]			
June	103 ± 13	82 ± 12	77 ± 4
July	103 ± 14	66 ± 10	64 ± 3
August	97 ± 15	54 ± 11	55 ± 4
Early September	86 ± 15	66 ± 13	75 ± 3

[a] $n = 18$ sites.
[b] $n = 9$ sites.

sites, which were not prebaited, were treated with strychnine oats on 24 September 1983. Three days after application the percentage of poisoned oats remaining on each burrow in a 1-ha grid on each treated site was estimated visually.

Statistical Evaluation

Analysis of covariance was used to compare each treated group (cluster) of sites with its respective control group. Applications of repeated measures were examined but required constant response through time—no interaction between time and treatment. These data did not show a constant response through time and had interactions; therefore, we used covariance adjustments. Pretreatment observations were used as covariates. Effect of rodenticide treatment for each time point was estimated as the covariance-adjusted difference between treated and control sites for each rodenticide. After obtaining an overall rejection of the hypothesis of no treatment effect, contrasts for each rodenticide treatment were evaluated for significance based on a variance estimated only from the sites in each cluster (because variance was heterogeneous among clusters). If the correlation between pretreatment and posttreatment observations was not significant ($\alpha \leq .20$), then the change was estimated as posttreatment minus pretreatment observation (repeated measures). This analysis uses the interaction between time and treatment as the indicator of a significant change due to treatment (Green 1979). Rodenticides were compared by forming pairwise contrasts of the contrasts obtained for the individual rodenticide treatments. Randomization procedures (Edgington 1980, Romesburg 1981) based on 10,000 random permutations of the data pairs among treatment groups were used to estimate statistical significance of the various contrasts.

Because omission of any effect due to poisoning was considered more serious than the potential incorrect declaration of a significant treatment effect, Type II error protection was produced by testing each contrast individually. However, some Type I error protection was afforded by testing individual contrasts only after first observing a significant ($P = .10$) overall test of treatment differences using analysis of covariance (Carmer and Swanson 1973). Individual contrasts were considered biologically significant at $P = .20$. Although admittedly unconventional for the number of sites available for study, this significance criterion produces a power (probability of detecting a true difference) of approximately 0.80 for a contrast twice as large as its standard error. This was considered a reasonable combination of Type I and Type II error protection for this study (Carmer 1976).

RESULTS

Prairie dog burrow activity declined during the summer months both years (Table 1). In June 1983 the number of active burrows was high (81%) and decreased steadily until late September, when 35% of the burrows were active. In June 1984 activity of prairie dog burrows was high (77%) and decreased through July and August, but increased to 75% in September.

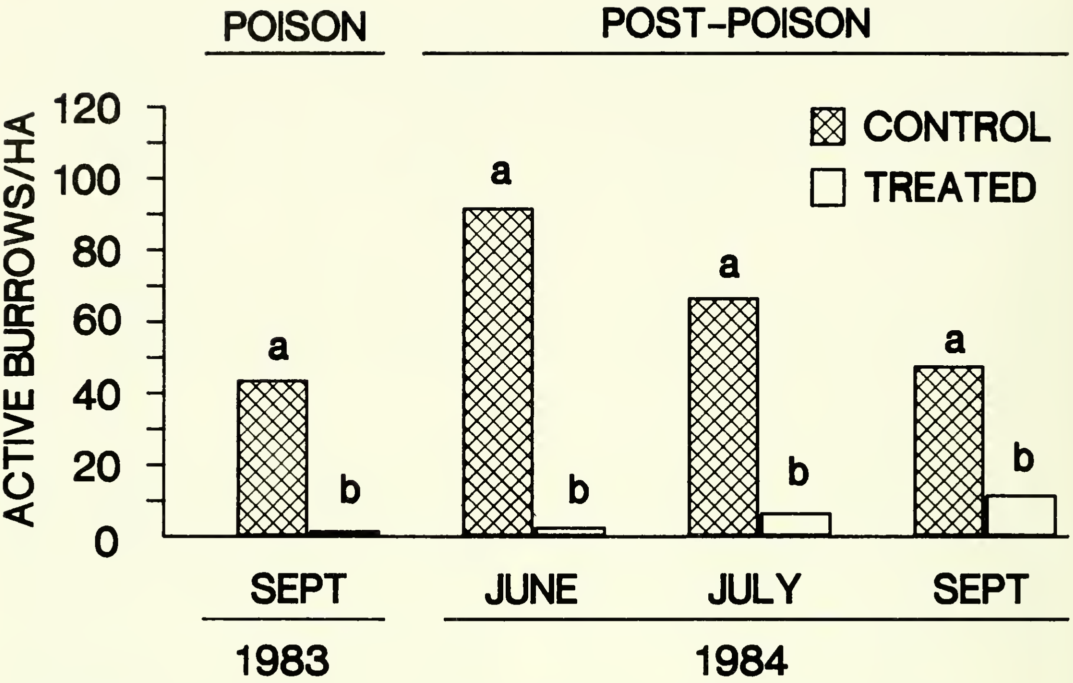

Fig. 1. Seasonal comparisons of active black-tailed prairie dog burrows on zinc phosphide-treated and control sites from initial treatment in September 1983 through September 1984. Means followed by the same letter by date are not significant at $\alpha = .20$ after F-protection at $\alpha = .10$ using analysis of covariance. (Data on September 1983 for initial poison are adapted from Uresk et al. 1986.)

In September 1983, immediately after treatment with zinc phosphide, the number of active prairie dog burrows was reduced 95% from the number on the 76 control sites ($P = .017$, Fig. 1). The reduction in the number of active burrows was maintained (96%) in June 1984 ($P = .002$). Reductions of active burrows in July and September were 92% and 77%, respectively ($P = .006$ and .014, respectively).

Treatment with strychnine only immediately reduced active burrows by 45% ($P = .164$, Fig. 2). In June 1984 active burrows on the treated sites remained 45% below the strychnine control sites ($P = .177$). By July, however, the number of active burrows on the treated sites was not different from the control sites ($P = .706$). The treated and control sites also showed similar burrow activity levels in September ($P = .637$).

Treatment with prebaited strychnine immediately reduced the number of active burrows by 83% ($P = .035$, Fig. 3). Burrow activity remained 85% below controls ($P = .019$) in June 1984. This reduced level of prairie dog activity compared with controls reached 99% in July and 95% in September 1984 ($P = .083$ and .057, respectively).

A comparison of the effectiveness of rodenticide treatments at initial poisoning of prairie dogs in 1983 showed that number of active burrows was reduced more with zinc phosphide than with strychnine alone ($P = .034$, Table 2). Burrow counts in June 1984 showed that towns with zinc phosphide treatment had fewer ($P = .006$) active burrows than those with strychnine only treatment. Similar results continued through July ($P = .035$) and September ($P = .039$) 1984.

Zinc phosphide had a greater initial effect than prebaited strychnine in reducing numbers of active burrows ($P = .075$, Table 2). There were no differences between the effects of the two rodenticides by 1984, however ($P = .20$).

When the two strychnine treatments were compared, reduction in active burrows was not different ($P = .391$) in September 1983 (Table 2). Strychnine compared with prebaited strychnine treatment in June 1984 showed a significant difference of 60 more

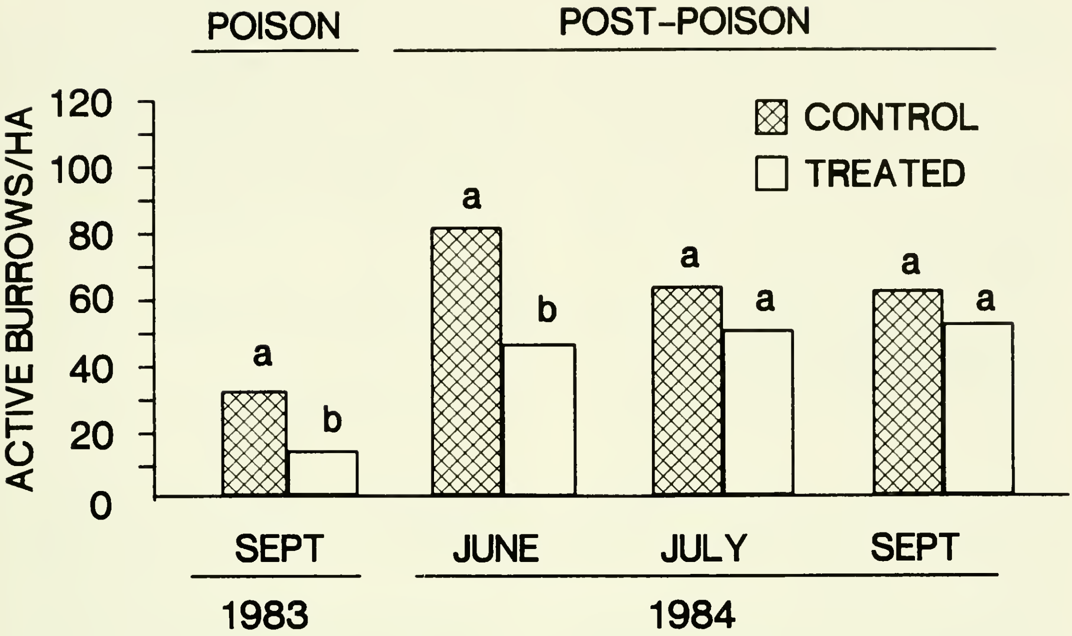

Fig. 2. Seasonal comparisons of active black-tailed prairie dog burrows on strychnine-only-treated and control sites from initial treatment in September 1983 through September 1984. Means followed by the same letter by date are not significant at α = .20 after F-protection at α = .10 using analysis of covariance. (Data on September 1983 for initial poison are adapted from Uresk et al. 1986.)

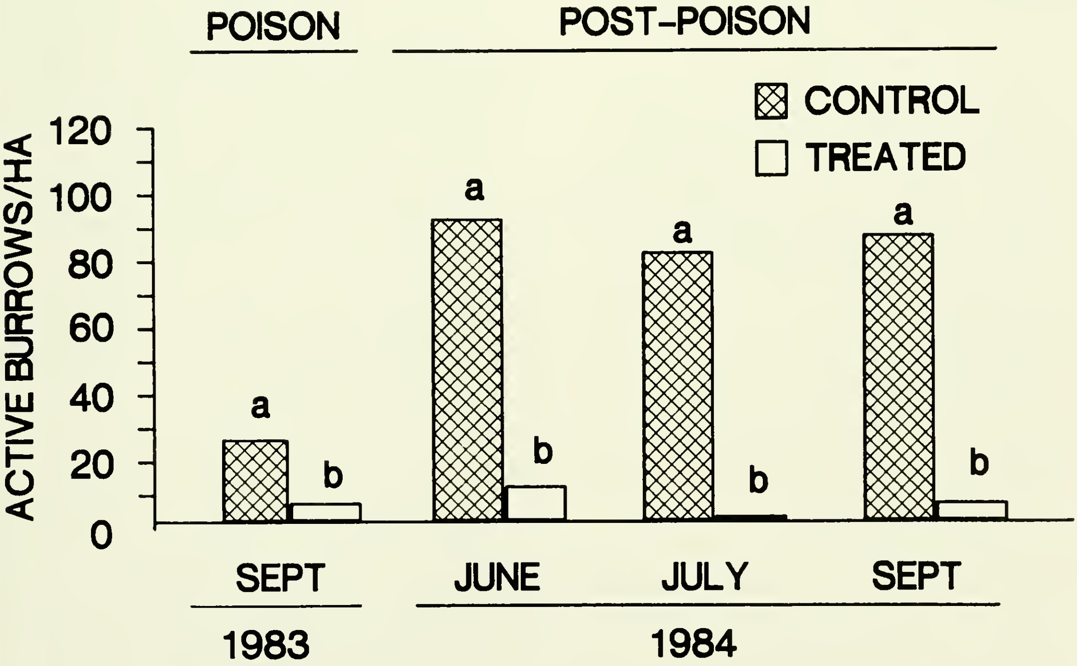

Fig. 3. Seasonal comparisons of active black-tailed prairie dog burrows on prebaited strychnine-treated and control sites from initial treatment in September 1983 through September 1984. Means followed by the same letter by date are not significant at α = .20 after F-protection at α = .10 using analysis of covariance. (Data on September 1983 for initial poison are adapted from Uresk et al. 1986.)

Table 2. Effectiveness of black-tailed prairie dog control with zinc phosphide (ZnP) compared with strychnine without prebait (S-9) and strychnine with prebait (PS-9), and strychnine without prebait compared with strychnine with prebait through time (active burrows/ha ± SE).

	Zinc phosphide versus strychnine only and prebaited strychnine								Strychnine only versus prebaited strychnine			
Period	ZnP[a]	S-9[a]	Main effect[b]	Signif[c]	ZnP[a]	PS-9[a]	Main effect[b]	Signif[c]	S-9[a]	PS-9[a]	Main effect[b]	Signif[c]
1983												
Sept	−45 ± 9	−14 ± 8	−31 ± 15	0.034	−45 ± 9	−23 ± 6	−22 ± 16	0.075	−14 ± 8	−23 ± 6	9 ± 11	0.391
1984												
June	−86 ± 2	−22 ± 12	−64 ± 9	0.006	−86 ± 2	−82 ± 13	−4 ± 9	0.872	−22 ± 12	−82 ± 13	60 ± 5	0.029
July	−59 ± 1	10 ± 6	−69 ± 7	0.035	−59 ± 1	−67 ± 32	9 ± 33	0.775	10 ± 6	−68 ± 32	78 ± 26	0.078
Sept	−42 ± 4	−7 ± 8	−38 ± 10	0.039	−42 ± 4	−77 ± 28	−33 ± 31	0.358	−7 ± 8	−77 ± 28	69 ± 26	0.062

[a] Effect adjusted using analysis of covariance.

[b] Main effect calculated by difference of poisons.

[c] Probabilities calculated for contrasts in randomization test (α = .20) based on variance heterogeneity after a significant F-protection at α = .10 by analysis of covariance.

active burrows (*P* = .029). Similar results continued throughout 1984 in July (*P* = .078) and September (*P* = .062).

Four days after treatment, prairie dogs had consumed more zinc phosphide than strychnine (*P* = .036) or prebaited strychnine (*P* = .012). Prairie dogs consumed 72 ± 7% (± SE) of the poisoned oats on burrows treated with zinc phosphide. Of oats treated with strychnine and prebaited strychnine, 16 ± 2% and 8 ± 1% were consumed, respectively.

Discussion

Densities of black-tailed prairie dog burrows on our study areas were similar to those reported earlier for South Dakota and other western states (Bailey 1926, Koford 1958, Uresk et al. 1982, O'Meilia et al. 1982, Uresk and Bjugstad 1983). Activity levels of prairie dogs have not been reported in the literature but are greatest in the spring when young-of-the-year become active. However, by fall many prairie dogs leave their towns, resulting in a reduction in burrow activity.

Prairie dogs were reduced most effectively with the zinc phosphide treatment. The level of reduction in active burrows achieved with zinc phosphide in the fall of 1983 was maintained through September 1984. Tietjen (1976a), Knowles (1982), and Tietjen and Matschke (1982) reported similar levels of reduction with zinc phosphide immediately after poison application. When strychnine only was applied, burrow activity was moderately reduced, but recruitment of prairie dogs increased the number of active burrows to precontrol levels by the following summer. The strychnine application with prebait reduced burrow activity in 1983 more than strychnine only and maintained reduced populations through September 1984.

The level of prairie dog reductions achieved with the zinc phosphide and strychnine with prebait treatments allowed minimal prairie dog recovery on towns, while reductions in prairie dog activity with strychnine alone were inconsistent. Knowles (1982) stated that the intrinsic rate of growth for prairie dogs in poisoned colonies was higher than normal. Prairie dog colonies with complete control required five years or more to return to precontrol densities. However, when a colony was partially treated, precontrol densities returned in two years. More bait remained on the prairie dog mounds after poisoning with strychnine than on mounds treated with zinc phosphide. Crabtree (1962) related prairie dog consumption of oats treated with rodenticides to the "taste factor" that accompanies strychnine and zinc phosphide and the time factor involved before there is a toxic reaction after poison consumption. Prebait is applied to increase the acceptance of a foreign food (grain bait); however, prairie dogs do not consume large amounts of strychnine because of its bitter taste and fast toxic reaction (5–20 minutes, Crabtree 1962). Rodents are attracted to the strong, pungent, phosphorus-like odor of zinc phosphide, and the toxic reaction is slower (Crabtree 1962), thus allowing more consumption of grain.

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EFFECTS OF BURNING AND CLIPPING ON FIVE BUNCHGRASSES IN EASTERN OREGON

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ABSTRACT.—Response of five perennial bunchgrasses following clipping and burning was evaluated in eastern Oregon. Burned plants were compared with clipped plants on several dates from spring to fall with respect to mortality and change in basal area. Basal area was generally reduced for one year but did not change the second year after defoliation. Treatments rarely affected yield. Burning in May was most detrimental, reducing basal area of all species. Fall clipping was least harmful, producing little or no change in basal area. Plant mortality was significant only for burned Thurber needlegrass (*Stipa thurberiana*).

Bunchgrasses comprise a major proportion of herbaceous vegetation in the Great Basin; yet little information is available regarding their response to defoliation. Furthermore, reports of bunchgrass response to fire and/or clipping are variable within and between species. Differences in defoliation effects are probably largely due to differences in growth form, phenology, season of treatment, and favorability of study years (Wright and Bailey 1982).

Bluebunch wheatgrass (*Agropyron spicatum*), Idaho fescue (*Festuca idahoensis*), junegrass (*Koeleria cristata*), bottlebrush squirreltail (*Sitanion hystrix*), and Thurber needlegrass (*Stipa thurberiana*) are dominant herbaceous species in eastern Oregon (botanical nomenclature follows Hitchcock and Cronquist [1973]). Published data concerning response of these species parallel that of most bunchgrasses in scarcity and variability. Appropriate management of these and other bunchgrass communities requires knowledge of their response to defoliation. The objective of this study was to evaluate the effects of fire on these five perennial bunchgrasses on eastern Oregon rangeland.

METHODS

The study area is located on Squaw Butte Experiment Station, 65 km west of Burns, Oregon. Elevation is 1,370 m, and average annual precipitation is 29.4 cm. Precipitation during the study was 24.6 cm in 1976, 27.5 cm in 1977, and 28.0 cm in 1978. Soil on the study area is a fine-loamy, mixed, frigid Aridic Durixeroll.

A 1-ha area was fenced to exclude livestock, and 90 plants each of five species were marked with wire stakes. Ten plants received no defoliation treatment and were treated as controls for mortality assessment. Ten randomly selected plants were burned with an individual plant burner (Britton and Wright 1979) on each of three dates: 15 May, 15 June, and 11 November 1976. Time-temperature curves peaked at 200 C at 30 sec. Ten randomly selected plants were clipped to 1-cm stubble height on each of the three dates. These clipped plants served as controls for burning treatments to evaluate the effects of fire separately from the effects of aboveground biomass removal. An additional 10 plants were clipped on 27 August and 12 October to compare effects of defoliation during late summer and early fall with other defoliation dates.

Treatment effects were measured as percentage changes in basal area and yield. After treatment each plant was photographed to determine initial basal area (cm^2). A wire grid (2.5 × 2.5 cm) was placed atop each plant base before photographing to provide a permanent record of basal area. Aboveground biomass

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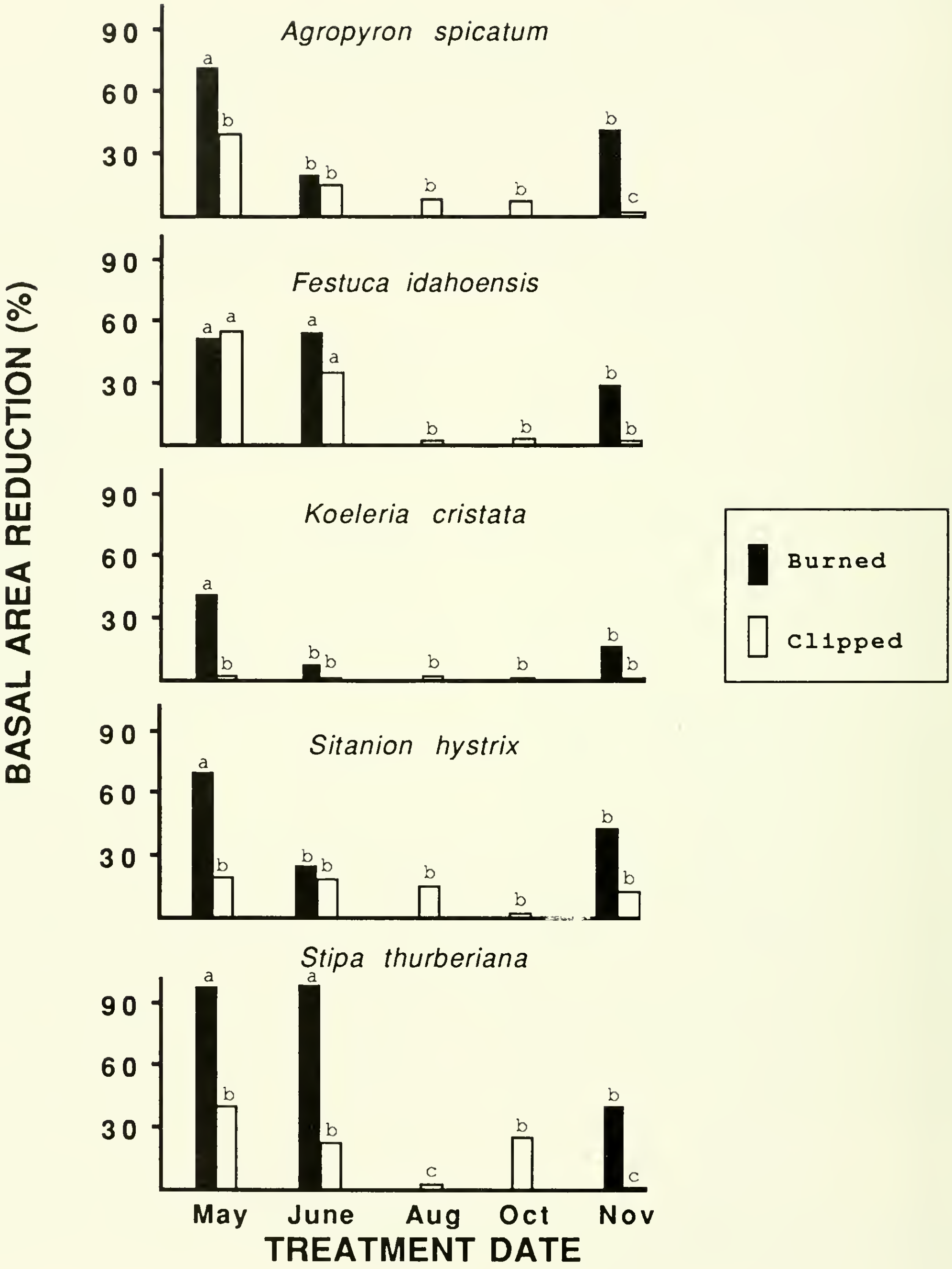

Fig. 1. Mean reduction in basal area of five bunchgrasses one year after burning or clipping in eastern Oregon. Plants were treated on various dates in 1976; basal area was measured immediately following treatment and in July of 1977 and 1978. Basal area reduction two years after burning rarely differed ($P > .05$) from 0%. Within a species, histograms marked with the same letter are not significantly different ($P > .05$).

was clipped in late July one and two growing seasons after treatment, and each plant was rephotographed at that time. Percentage change in basal area was calculated, and analysis of covariance (adjusted to initial plant basal area) was used to test for differences in basal area among treatments one year and two years posttreatment. Yield was expressed as grams per square decimeter of basal area to adjust for different plant sizes. Plants with no live tillers two years after treatment were assumed to be dead. Means were separated using Fisher's protected LSD test ($P = .05$).

RESULTS

Basal Area

Basal area generally declined the first year after treatment (Fig. 1). Bluebunch wheatgrass basal area decreased 45% one year after burning and 22% after clipping. May burning was especially damaging to basal area (−69%); by contrast, November clipping had no effect on basal area. Other treatment-date combinations were intermediate (mean = −32%) and did not differ. Effects of August and October clipping treatments (mean = −13%),were intermediate between effects of May and June clipping (mean = −28%) and November clipping (no change).

Idaho fescue basal area was affected by date of defoliation but did not differ between treatments. Defoliation in May and June reduced basal area by an average of 48%. Other treatment-date combinations did not significantly ($P > .05$) reduce basal area.

Basal area of junegrass was reduced 42% by burning in May. No other treatment-date combinations differed significantly from 0%.

Squirreltail basal area was reduced 71% by burning in May, which was a greater reduction than other treatment-date combinations (mean = −24%). Basal area change of plants clipped in August, October, and November did not differ significantly from 0%, indicating that squirreltail was resistant to late-season clipping.

Needlegrass basal area was reduced 93% by May and June burning, largely due to high mortality associated with early burns (May mortality = 50%, June mortality = 70%). August and November clipping treatments did not significantly affect basal area. Change in basal area did not differ between other defoliation treatments (mean = −33%), which were intermediate between early-season burning and late-season (August, November) clipping treatments.

Subsequent (second-year) decreases in basal area of all species were slight and generally not significant ($P > .05$) and will not be discussed. Exceptions were (1) junegrass, which decreased the second year following burning (mean = −21% from first year to second) or clipping (mean = −18%) on all dates; (2) squirreltail, which decreased following burning in May (−53%) and June (−42%); and (3) needlegrass, which decreased following clipping in August (−27%).

Yield

Yield (adjusted for basal area) of bluebunch wheatgrass was not affected by method or date of defoliation. First-year yield was 4.2 g/dm^2; second-year yield was 7.3 g/dm^2 (Fig. 2).

First-year yield of Idaho fescue was reduced by date of defoliation, but clipping and burning did not differentially influence yield. Plants defoliated in May produced 6.1 g/dm^2 dry matter, compared with a mean yield of 3.1 g/dm^2 for all other dates. Yields from supplementary August and October clipping treatments did not differ from June and November yields. Second-year yield (mean = 8.0 g/dm^2) was not affected by date or method of defoliation.

First-year yield of junegrass was affected by defoliation date in a manner similar to that of Idaho fescue. Defoliation in May resulted in 2.7 g/dm^2 dry matter production, compared with 1.5 g/dm^2 following defoliation in November. Yield following clipping in October was 1.8 g/dm^2, which was lower than yield following May defoliations. Yields from June and August treatments were intermediate (mean = 2.3 g/dm^2) and did not differ from yields on other dates. Second-year yields were unaffected by date or method of defoliation (mean = 7.0 g/dm^2).

Squirreltail yield was lower one year after burning (1.6 g/dm^2) than after clipping (5.8 g/dm^2) in May. A significant treatment × date interaction precluded comparisons across all dates. Yields following burning and clipping did not differ on other dates, and date of defoliation did not affect yield of clipped plants (mean = 4.7 g/dm^2). Second-year yield was

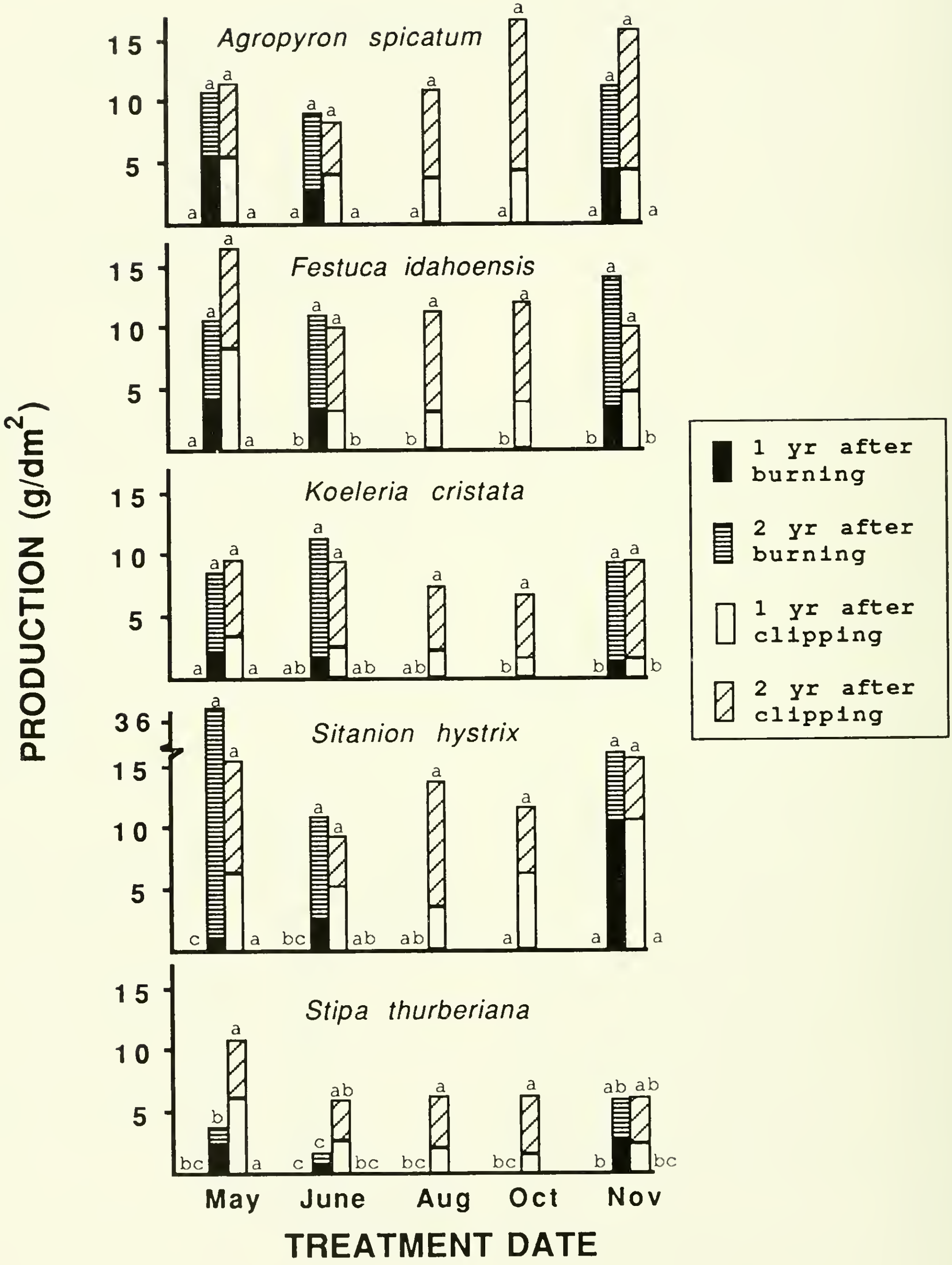

Fig. 2. Mean production of five bunchgrasses one and two years after burning or clipping in eastern Oregon. Plants were treated on various dates in 1976; aboveground biomass was clipped in July of 1977 and 1978. Within a species, histograms marked with the same letter are not significantly different ($P > .05$).

not affected by date or method of defoliation (mean = 12.3 g/dm^2).

First-year yield of needlegrass was affected by date and method of defoliation; the date × treatment interaction was also significant. Yield following clipping in May was higher than any other date-treatment combination (6.4 g/dm^2). Mean yield following November burning was higher than after June burning (2.6 vs. 0.6 g/dm^2), largely due to higher survival of fall-burned plants (90 vs. 30%). First-year yields of other date-treatment combinations were intermediate (1.9–2.5 g/dm^2) and did not differ. Needlegrass was the only species in which second-year yield was affected by treatment. Mean second-year yields of burned and clipped plants were 2.0 and 4.2 g/dm^2, respectively. Increased mortality of burned plants (mean = 57%) accounted for the difference. Second-year yield was not affected by date of defoliation. Needlegrass was the only species in which significant mortality occurred. Burning in May, June, and November resulted in 50%, 70%, and 10% mortality, respectively. No control or clipped plants died.

DISCUSSION

Bluebunch wheatgrass was relatively tolerant to all treatments except May burning. Basal area declined more following burning than clipping, but yield responses were similar between treatments. Similarly, Uresk et al. (1976) reported decreased basal area and increased yield one year after a wildfire in eastern Washington. Conrad and Poulton (1966) found a 29% reduction in basal area one year after a wildfire in the same area. Wright (1985) summarized the literature on grass response to fire in sagebrush-grass communities and concluded that bluebunch wheatgrass is slightly affected by burning, with yield returning to preburn levels in one to three years.

Idaho fescue appeared to be less susceptible to defoliation than has been reported previously. Basal area and mortality were not affected by late summer or fall defoliation. Furthermore, burning and clipping had similar effects on plants. Wright et al. (1979) summarized studies by Pechanec and Stewart (1944), Blaisdell (1953), Countryman and Cornelius (1957), Conrad and Poulton (1966), and Harniss and Murray (1973), stating that "the majority of evidence indicates that Idaho fescue is severely damaged regardless of when or where it is burned." However, Wright (1971) found increased resistance to burn damage from late July through late September, and attributed the altered resistance to low energy reserves and high respiration demands during late summer. Daubenmire (1970, 1987) reported mixed results for wildfires in eastern Washington. Wright and Klemmedson (1965) reported minimal damage to Idaho fescue after late-summer and fall fires; data from this study indicate that late-season defoliation may not be harmful at all. Higher yields of plants defoliated in May are attributable to (1) decreased basal area with no decrease in yield per plant, and (2) decreased growing period for plants treated later in the growing season. Plants treated after 15 May had begun growth at the time of defoliation. Second-year yield was not affected by date or method of defoliation, further indicating that the additional growing period associated with early defoliation produced the observed differences in first-year yield. Britton et al. (1983) found that first-year yields of Idaho fescue following August burning were 25% lower than yields following burning in October.

Junegrass was tolerant to all treatments except May burning. Basal area decreased in the second year after defoliation, although production increased. Wright et al. (1979) attributed junegrass's resistance to the relatively small size of typical junegrass plants. Relatively high yields following early defoliation and low yields following late defoliation support the hypothesis that yield is influenced primarily by length of growing season following defoliation. Further support was provided by second-year yields that were unaffected by date or method of defoliation.

Squirreltail was moderately affected by defoliation, with significant basal area decreases in all treatments except late-season clipping. May burning was most detrimental to basal area. Wright (1971) reported similar results in southern Idaho and attributed squirreltail's late-season tolerance to clipping to summer dormancy (Wright 1967). Young and Miller (1985) found no change in basal area, but increases in above- and belowground yield, following July burning. Squirreltail's resistance to fire derives from plant growth form (coarse stems with little leafy material) and small size (which precludes development of dead centers) (Wright and Bailey 1982, Daubenmire 1987). Since basal area decreased by an average of 47% the second year after early-season burns, increased abundance on burned areas (Blaisdell 1953, Barney and Frischknecht 1974) probably results from squirreltail's ability to survive and subsequently invade sites previously occupied by other perennial plants, and not from increased size of individual plants. Lack of differences in yield two years after defoliation indicated that response of squirreltail, along with bluebunch wheatgrass, Idaho fescue, and junegrass, varied independently of the method of defoliation.

Needlegrass was severely damaged by all defoliation treatments. Burning was particularly harmful, increasing mortality and reducing mean basal area and yield. Uresk et al. (1976) reported a 53% reduction in basal area following an August wildfire; recovery was not complete three years later (Uresk et al. 1980). Wright et al. (1979) concluded that Thurber needlegrass is probably the least resistant needlegrass. Early-season clipping was more damaging to needlegrass than late-season clipping in this study. Plants responded similarly to May, June, and August clipping and November burning, but later clipping treatments had no measurable effect.

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FOLIAGE BIOMASS AND COVER RELATIONSHIPS BETWEEN TREE- AND SHRUB-DOMINATED COMMUNITIES IN PINYON-JUNIPER WOODLANDS

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ABSTRACT.—Woodlands dominated by singleleaf pinyon (*Pinus monophylla* Torr. and Frem.) and Utah juniper (*Juniperus osteosperma* [Torr.] Little) cover extensive areas in the Great Basin and Southwest. Both species are aggressive and can nearly eliminate the previous shrub-dominated community. Successional pathways from shrub-dominated communities before tree establishment to the tree-dominated communities that follow are known only for a few specific sites. How site growing conditions affect successional patterns needs further study. We compared the relationship of foliage biomass and percentage of cover between paired shrub-dominated and tree-dominated plots over several sites. Sites studied are from different elevation and topographic conditions on one mountain range. Foliage biomass in shrub-dominated plots had about a three-to-one variation over the range of site conditions sampled. Tree-dominated plots varied by about two to one. Cover in shrub-dominated plots had a four-to-one variation; cover in the tree-dominated plots varied by about two to one. Total foliage biomass in both tree- and shrub-dominated plots correlated best with the site index of height at 200 years of age. Variation in percentage of cover in both tree- and shrub-dominated plots correlated best with elevation. Foliage biomass variation in shrub-dominated plots was proportional to the variation in the paired tree-dominated plots. A similar proportional relationship was present for percentage of cover between paired tree- and shrub-dominated plots. Foliage biomass was more sensitive to topographic differences than to cover. Variation in plant species sampled in the shrub-dominated plots correlated with total foliage biomass of the same plots. Species sampled also correlated with pinyon height at 200 years of age and total foliage biomass in the paired tree-dominated plots.

Singleleaf pinyon (*Pinus monophylla* Torr. and Frem.) and Utah juniper (*Juniperus osteosperma* [Torr.] Little) woodlands cover more than 72,000 km^2 (18 million acres) in the Great Basin, coverage greater than it was before European settlement (Tausch et al. 1981). Both species are successionally aggressive and, once established, can nearly eliminate the understory. Loss of forage and increased soil erosion can result from dominance by the trees (Doughty 1987). Established woodlands provide wood products, pine nuts, and habitat for many wildlife species.

Successional pathways from shrub-dominated communities before tree establishment to the resulting tree-dominated communities that follow are known from only a few specific sites (Barney and Frischknecht 1974, Tausch et al. 1981, Young and Evans 1981, Everett and Ward 1984, Everett 1987). Variability in both tree- and shrub-dominated communities (Ronco 1987) complicates extrapolation of these results to sites of different growing conditions. Comparisons of biomass and cover relationships between shrub- and tree-dominated communities on the same sites are needed for more locations.

Woodlands have a higher percentage of cover at higher than at lower elevations and on north than on south aspects (West et al. 1978, Tueller et al. 1979). Both tree- and shrub-dominated communities appear to show an increase in cover, and in biomass, on the better sites. The potential three-dimensional form of these relationships is illustrated in Figure 1. Orientation of the X, Y, and Z axes in Figure 1 is for clarity of presentation of the three-dimensional representation.

The vertical X axis represents improving site conditions. Increasing cover or biomass in tree-dominated communities is represented by the Y axis. The Z axis represents increasing cover or biomass in shrub-dominated communities. The line a–e (Fig. 1) represents the relationship between site and shrub cover or biomass. The line a′–e′ represents the same relationship with site for biomass or cover of tree-dominated communities. If the relation-

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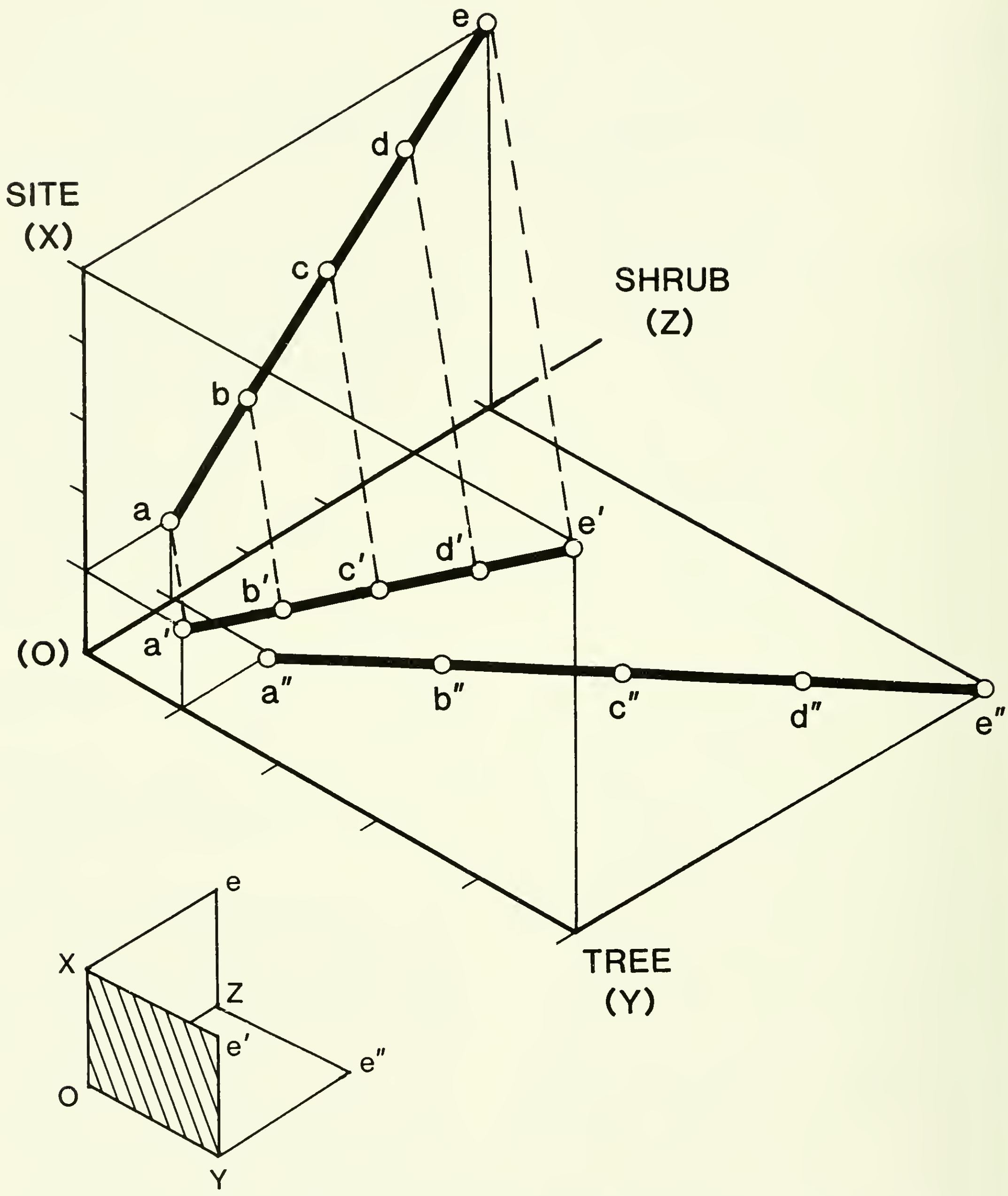

Fig. 1. Three-dimensional representation of hypothesized relationships between site quality (X) and cover or biomass in tree- (Y) or shrub-dominated (Z) communities in pinyon-juniper woodlands. The lines a–e, a′–e′, and a″–e″ represent hypothesized relationships among the respective axes.

ships of the X–Y and Y–Z planes hold true, a relationship also exists on the Y–Z plane. This is a proportional relationship between the quantities in the shrub- and tree-dominated communities represented by the a″–e″ line.

The a–e–e′–a′ plane (Fig. 1) represents the family of successional pathways for these communities for the site conditions represented. Succession in these woodlands without disturbance proceeds from shrub to tree domination

(Tausch et al. 1981). Dotted lines a–a′ through e–e′ estimate specific pathways for each site class. These pathways are drawn linearly only for visibility. They usually follow various types of curvilinear patterns (Tausch et al. 1981).

This study investigated the hypothesized three-dimensional relationship between cover or biomass of tree- and shrub-dominated communities and site. The X-Y, X-Z, and Y-Z planes in Figure 1 represent these relationships. Analyses used the total foliage biomass and total percentage of cover of tree-dominated and shrub-dominated communities of several sites on one mountain range. Sampled sites cover a range of elevational and topographic conditions.

Percentage of total vegetal cover has broad use in many other studies in these communities. Total foliage biomass (which can be directly related to leaf area) was included because it is a community dimension that reaches an equilibrium level in many forest types (Moller 1947, Marks and Borman 1972, Long and Turner 1975, Long and Smith 1984). More mesic sites than drier sites support higher equilibrium biomass (Waring et al. 1978). Equilibrium leaf biomass levels can be directly related to the hydrologic environment (Nemani and Running 1989). Other studies have also shown equilibrium levels of leaf biomass (or area) in relationship to site moisture conditions (Whittaker and Niering 1975, Grier and Running 1977) and nutrient stress (Waring et al. 1978). Only the endpoints of the potential sere on each site were sampled to increase the number of sites available.

METHODS

Data Collection

This study used six sites on the Sweetwater Mountains, Nevada and California (Table 1). We sampled a tree-dominated and a shrub-dominated plot at each site. The tree-dominated plots were fully stocked or fully tree-occupied as defined by Meeuwig and Cooper (1981). Shrub-dominated plots did not have trees larger than seedlings. These seedlings were less than 3 dm tall. Tree- and shrub-dominated plots were paired on each site on the same slope, aspect, and elevation. Plots were as close as physically possible while still meeting the criteria for tree or shrub dominance.

TABLE 1. Aspect, slope, and elevation (m) for the six sample sites on the Sweetwater Mountains, Nevada and California. Plot identifications for tree-dominated plots from Meeuwig (1979) are in parentheses next to the site number.

Site	Aspect (degrees)	Slope (degrees)	Elevation (m)
1	81	3	2,120
2	75	2	2,030
3	90	4	2,280
4(S1)	80	3	2,210
5(S3)	120	9	2,300
6(S4)	345	20	2,020

TREE PLOT DATA.—Tree data for tree-dominated plots for three sites (4–6, Table 1) are from Meeuwig (1979) and Meeuwig and Budy (1979). We sampled additional tree-dominated plots on sites 1–3 (Table 1) to extend the elevational and topographic range of the data. All tree-dominated plots had only pinyon, except site 6, which had some juniper. Sites 2, 1, 4, and 5 represent a transect up the east side on the main alluvial fan and mountain slope of the Sweetwater Mountains. The sites cover the width of the woodland belt at about 100-m-elevation intervals. Site 3 is on the flat top of a foothill away from the main mountain mass, site 6 on a north-facing slope in a narrow canyon.

Tree-dominated plots for sites 1, 2, and 3 (Table 1) were 20 × 50 m in size (0.1 ha). We measured all trees in each plot for average crown diameter, tree height, and basal diameter about 15 cm above the ground surface. Where multiple trunks were present, we individually measured each trunk and determined a geometric average basal diameter (Meeuwig and Budy 1979). Tree foliage biomass and trunk cross sections were collected from a random sample of 12–14 trees in each plot (Tausch and Tueller 1988, 1989). These trees were aged by ring counts on two radii of their cross sections.

Tree-dominated plots for sites 4–6 from Meeuwig (1979) and Meeuwig and Budy (1979) were 30 × 30 m in size. All trees in each plot were measured using the methods described above and harvested. A random sample of the harvested trees was weighed to determine total wet and dry biomass for bole, bark, branch, twig, and foliage. Multiple regression techniques were used to derive the total dry biomass values for each part and the total of the remaining trees on each plot from their measurements. Meeuwig and Budy (1979) aged all trees by ring counts. We extrapolated their leaf biomass data to a 0.1-ha plot size.

As a part of this study, we collected additional tree foliage biomass data from a random sample of trees adjacent to the plots from Meeuwig (1979) and Meeuwig and Budy (1979). These data were collected by the same techniques used for the tree-dominated plots on sites 1–3. Analysis results from these trees were used as an independent test of the foliage biomass predictions (Tausch and Tueller 1988).

Shrub plot data.—Suitable shrub-dominated areas without mature trees varied in size between sites. Shrub-dominated plots on sites 1, 2, and 4 were 20 × 50 m (0.1 ha) in size. The largest shrub-dominated area on site 3 permitted a 15 × 30-m plot. Adjacent shrub-dominated areas of the same environmental conditions were not present for sites 5 and 6. A strong recovery by the understory was present in the plot areas originally cleared by Meeuwig (1979) and Meeuwig and Budy (1979) seven years earlier. Shrub-dominated plots 20 × 20 m in size were centered in their former tree plots.

We used five transects to sample plant species data on all shrub-dominated plots except site 3. These transects were 20 m long and randomly located perpendicular to the plot axis. Each transect contained 10 contiguous 1 × 2-m microplots, for a total of 50 microplots. Site 3 was sampled with seven randomly located transects 14 m long. Each transect was divided into seven 1 × 2-m microplots, for a total of 49 microplots. Although the overall plot size varied, the number of microplots sampled was equivalent for all the shrub-dominated plots.

The same techniques used in the 20 × 50-m shrub-dominated plots were used to collect understory data in the tree-dominated plots for sites 1, 2, and 3. Understory data were not available for the tree-dominated plots from Meeuwig (1979) and Meeuwig and Budy (1979).

We measured three crown dimensions on all shrub and perennial grass species in each microplot: (1) longest crown diameter, (2) diameter perpendicular to the longest, and (3) height of the foliage-bearing portion of the crown. A random selection of the sampled microplots was used to collect foliage biomass for the more common measured species. Foliage biomass was collected from 24 random individuals of the dominant and co-dominant shrubs and 12 random individuals of the subdominant species in each plot. We collected foliage biomass of infrequently occurring species on both tree- and shrub-dominated plots whenever they were present in any microplot. All measured species in the understory samples of the tree-dominated plots, except the dominant shrubs, were sampled whenever present in a microplot.

We estimated the foliage biomass of forb and annual grass species in each microplot using the reference unit method (Andrew et al. 1979, 1981, Kirmse and Norton 1985, Cabaral and West 1986, Carpenter and West 1987). Actual foliage biomass of reference unit species was also collected in the random sample of microplots. This collected foliage biomass data provided a double sampling correction on the reference unit estimates. Foliage biomass of infrequently occurring forb species was collected whenever such species were present in any microplot. Percentage of each plot covered by each species of forb and annual grass was estimated for each microplot and averaged.

Data Analysis

Tree plot data.—We determined relationships of basal area to tree foliage biomass of the randomly sampled trees in each plot by nonlinear allometric regression analyses (Tausch and Tueller 1988, Tausch 1989). Analysis results were used to estimate the foliage biomass of the remaining trees in each plot from their basal diameters. Individual tree foliage biomass values were summed, for a total tree foliage biomass in each plot. The process was repeated for the trees sampled next to the three plots from Meeuwig (1979) and Meeuwig and Budy (1979). We used our tree data to predict their total foliage biomass values as a check on the methodology (Tausch and Tueller 1988).

Five indices of site class were used for this study: (1) Site Index I, height at an age of 200 years; (2) Site Index II, height at a basal diameter of 25.4 cm; (3) tallest tree, height of the tallest tree on the plot; (4) average tree height, average height of dominant and co-dominant trees; (5) elevation, in meters of the sample site. Site Index I was determined by the techniques described by Aguirre-Bravo and Smith (1986). Their methods were successfully applied to pinyon in the New Mexico, Colorado, and Arizona area by Smith and Schuler (1988). This method uses the Chapman-Richards equation to fit the guide curve for a family of anamorphic site index curves. The equation is:

$$H = \theta_1 (1 - \exp(-\theta_2 A))^K \qquad (1)$$

where H = tree height, A = tree age, K = a constant equal to $1/(1-\theta_3)$, and θ_1, θ_2, θ_3 = parameters of the Chapman-Richards equation. Equation 1 was fitted to the combined tree height and age data for all the sampled tree-dominated plots by an iterative, nonlinear regression procedure (Caceci and Cacheris 1984).

The average age and height of the dominant and co-dominant trees were based on the entire plot for sites 4–6. On sites 1–3 these averages were based on the randomly sampled trees that were dominant or co-dominant. We determined Site Index I for each tree-dominated plot, using these averages in a site-prediction equation based on equation 1 (Aguirre-Bravo and Smith 1986).

$$S = H\left[\frac{(1 - \exp(-\theta_2 A_0))}{(1 - \exp(-\theta_2 A))}\right]^k \qquad (2)$$

where A_0 = the age of reference (200 years), A = the average age of the dominant and co-dominant trees, H = the average height of the dominant and co-dominant trees, and S = Site Index I.

The second measure of site class, tree height at a constant basal diameter of 25.4 cm (Site Index II), was from work in Nevada pinyon-juniper woodlands by Chojnacky (1986). Nonlinear regression (Caceci and Cacheris 1984) was used to fit the allometric equation (height = a(diameter)^b) to the diameter and height data for all trees in each plot. We determined Site Index Class II height from the equation for each plot for the diameter of 25.4 cm. The last three site indices, average height of dominant and co-dominant trees, height of the tallest tree, and elevation, were used directly.

TABLE 2. Nonlinear regression results for basal area to foliage biomass relationships for trees sampled in tree-dominated areas of six sample sites. Data for sites 4, 5, and 6 are also discussed in Tausch and Tueller (1988). Site designations are from Table 1.

Site number	Sample size	r^2	Standard error (kg)
1	12	.97	3.15
2	12	.85	7.89
3	14	.98	1.03
4(S1)	12	.88	7.81
5(S2)	12	.92	3.93
6(S4)	12	.93	4.19

SHRUB PLOT DATA.—Crown volumes for the measured shrub species are based on the equation for one-half of an ellipsoid. A cylinder was used for the perennial grasses (Tausch 1980, Johnson et al. 1988). We used a sum of crown areas to compute percentage of cover of the measured species on each plot. Allometric equations were derived from crown volume and foliage biomass data randomly collected for each measured species, using nonlinear regression (Johnson et al. 1988, Tausch and Tueller 1988, Tausch 1989). These equations were used with crown volume data for the remaining plants in each plot to estimate foliage biomass by species.

Foliage biomass data from crown measurement and reference unit methods were summed for individual species total leaf biomass in each shrub-dominated plot. We extrapolated all data to a 0.1-ha plot size. Understory data from the tree-dominated plots on sites 1, 2, and 3 were similarly treated.

TREE/SHRUB/SITE COMPARISONS.—We used regression and correlation analyses to compare all relationships among total foliage biomass, total percentage of cover, and the five indices of site class. Total foliage biomass, cover, and the five site indices were also compared with the number of species sampled in the shrub-dominated plots.

A foliage biomass ratio (percentage) of the total in the tree-dominated plots divided by the total in the paired shrub-dominated plots was computed for each site. We computed a similar ratio (percentage) for total percentage cover. These ratios were compared with the number of species sampled in shrub-dominated plots and with the five site class indices by correlation analysis.

Table 3. Coefficient of determination values (r^2) for equations to predict ratio of crown volume to foliage biomass for the sampled shrub and perennial grass species. The letter *a* indicates plots where foliage biomass was collected from all individuals occurring in the sampled microplots. Site numbers are from Table 1.

	Site number								
	Shrub-dominated plots						Tree-dominated		
Plant species	1	2	3	4	5	6	1	2	3
Artemisia tridentata vaseyana	.88		.81	.96	.95	.98	.91	a	a
A. tridentata wyomingensis		.87						.85	
Ceratoides lanata	.83			a	a				
Chrysothamnus viscidiflorus	a		a	.88	a				
Ephedra viridis					a		a		a
Eriogonum umbellatum				a	a				
Opuntia sp.				a					
Prunus andersonii	a			.96	.98		a		
Purshia tridentata	.99	.98	.96	.98	.78	.95	a	a	a
Ribes velutinum	.85			a	a		a		a
Symphoricarpos sp.									a
Elymus cinereus					.98				
Oryzopsis hymenoides			.87		a	a			
Poa sandbergii	.90		.81	.72	.95		a	a	a
Sitanion hystrix	.76	.86	.99	.81	.82	.86			
Stipa thurberiana	.87		.87	.86	a		a	a	

Table 4. Standard error of the estimate (g) for equations to predict ratio of crown volume to foliage biomass for the sampled shrub and perennial grass species. The letter *a* indicates plots where foliage biomass was collected from all individuals occurring in the sample microplots. Site numbers are from Table 1.

	Site number								
	Shrub-dominated plots						Tree-dominated		
Plant species	1	2	3	4	5	6	1	2	3
Artemisia tridentata vaseyana	33.2		15.5	31.3	3.68	1.76	7.13	a	a
A. tridentata wyomingensis		1.79						1.60	
Ceratoides lanata	1.28			a	a				
Chrysothamnus viscidiflorus	a		a	3.64	a				
Ephedra viridis					a		a		a
Eriogonum umbellatum				a	a				
Opuntia sp.				a					
Prunus andersonii	a			1.70	.59		a		
Purshia tridentata	1.51	1.38	7.74	1.25	41.8	1.30	a	a	a
Ribes velutinum	46.6			a	a		a		a
Symphoricarpos sp.									a
Elymus cinereus					19.4				
Oryzopsis hymenoides			.07		a	a			
Poa sandbergii	.09		.07	.08	.03		a	a	a
Sitanion hystrix	.21	.18	.20	.06	.14	.18			
Stipa thurberiana	.29		.29	.06	a		a	a	

Relationships between the foliage biomass components of the shrub-dominated plots were determined by correlation analysis. The components used were the total shrub, total perennial grass, total cheatgrass, and total forb leaf biomass, and the number of species sampled. These five shrub-dominated plot components were similarly compared with the total foliage biomass in the tree- and shrub-dominated plots and with the five site indices.

RESULTS AND DISCUSSION

Foliage Biomass Predictions

TREE DATA.—Prediction of pinyon total leaf biomass in Meeuwig's (1979) plots (4, 5, and 6, Table 1) using equations from trees we collected adjacent to those plots had an average error of +0.5% (Tausch and Tueller 1988). Equations for tree data on sites 1, 2, and 3 had coefficient of determination and standard error values very similar to those for sites 4, 5,

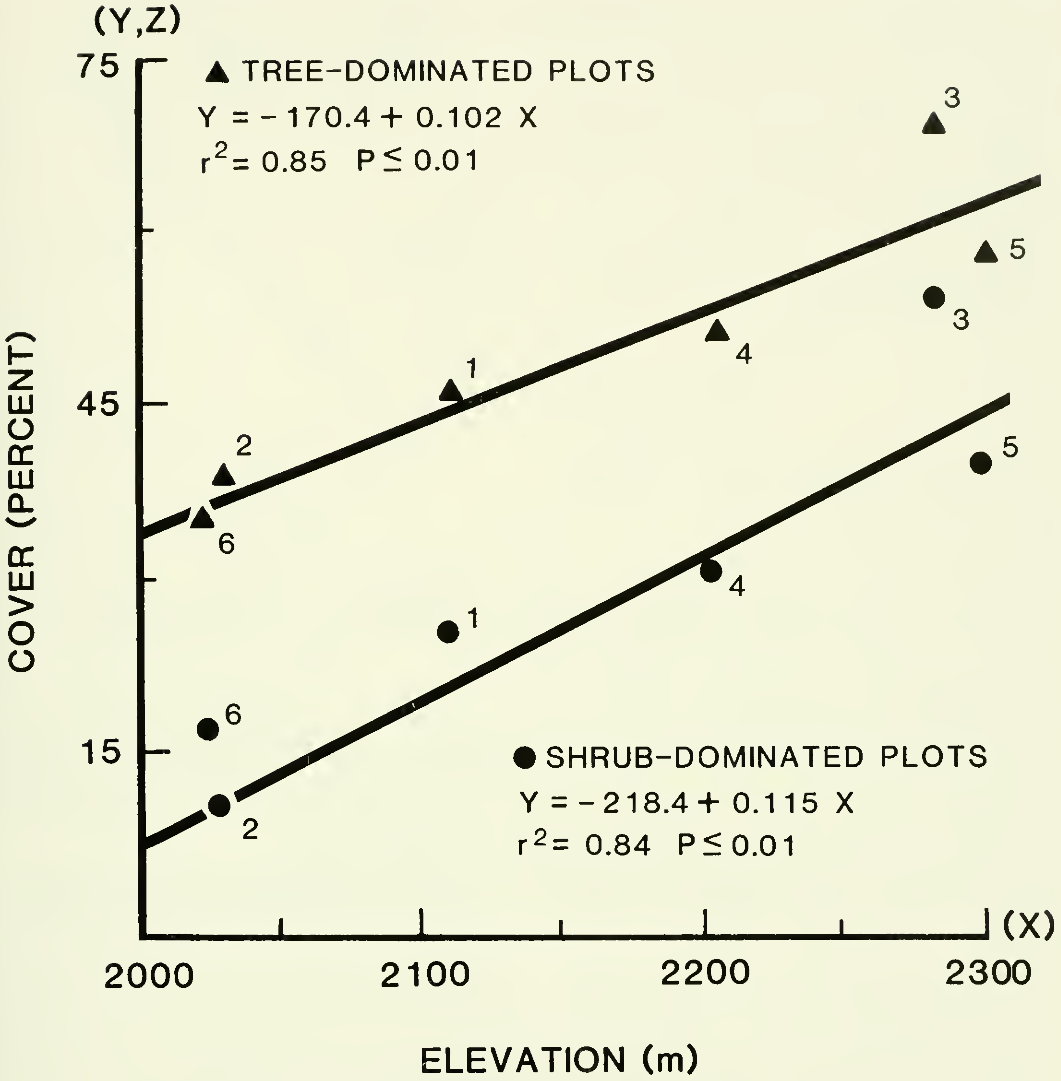

Fig. 2. Regression analyses between elevation and total percentage of cover in both tree-dominated plots and shrub-dominated plots. Axis designations follow those in Figure 1. Site numbers follow Table 1.

and 6 (Table 2). From these results we considered our tree data from sites 1, 2, and 3 to be similar enough to Meeuwig's (1979) tree data for sites 4, 5, and 6 for the data to be combined.

SHRUB, GRASS, AND FORB DATA.—Based on coefficient of determination (Table 3) and standard error of the estimate values (Table 4), prediction equations for the measured species have similar precision. Precision is also similar to the tree results (Table 2) and to other test results for sagebrush and bunchgrass foliage biomass (Tausch 1989). The measured shrub and perennial grass species averaged 98% of the total foliage biomass on the shrub-dominated plots. This combination also averaged more than 99% of the total foliage biomass of the understory in the three tree-dominated plots we sampled. Total understory foliage biomass on the tree-dominated plots averaged less than 0.50% of the total plot foliage biomass. We considered the error resulting from the lack of understory data for the three tree-dominated plots from Meeuwig (1979) and Meeuwig and Budy (1979) to be minimal.

Cheatgrass (*Bromus tectorum*) occurred on all sites and plots. Common forbs sampled included *Colinsia parviflora* and *Arabis holbolii* on all but site 2, and *Phlox longifolia* and *Descuriana pinnata* on all but sites 2 and 3. *Crepis accuminata*, *Lupinus caudatus*, *Lygodesmia spinosa*, and *Wyethia amplexicaulis* were present on sites 1, 4, and 5.

Site class index.—The final Site Index I parameter estimates for the Chapman-Richards equation after minimizing the residual sum of squares were:

$\theta_1 = 9.699$
$\theta_2 = 0.00764$
$K = 0.9342$
Residual sum of squares = 281.1
Standard error of the estimate = 1.488
Coefficient of determination = 0.65

These parameters were used in equation 2 to determine the Site Index I value for each tree-dominated plot. They ranged from 6.48 to 9.69 m. Site Index II values (height at 25.4 cm basal diameter) ranged from 4.08 to 6.34 m. The heights of the tallest trees in the plots ranged from 6.9 to 11.1 m. Average heights of the dominant and co-dominant trees ranged from 4.6 to 8.8 m. The asymptotic height for the combined Sweetwater Mountains data (θ_1) is over 2 m higher than for the combined pinyon data for Arizona, Colorado, and New Mexico (7.63 m) from Smith and Schuler (1988).

Tree and Shrub Plot Comparisons

Total percentage cover in the tree-dominated and shrub-dominated plots for the six sites positively correlated with the elevation (Fig. 2). Figure 2 represents both the X–Y and X–Z planes in Figure 1. They also positively correlated with each other (Fig. 3). Figure 3 represents the Y–Z plane in Figure 1. Percentage of cover did not significantly correlate with any of the other four site indices based on tree height or with the total foliage biomass in the respective tree- or shrub-dominated plots. Percentage of cover on a total plot basis apparently does not clearly reflect leaf biomass.

Total foliage biomass in both the tree-dominated and shrub-dominated plots positively correlated with Site Index I (Fig. 4) and with each other (Fig. 5). Total tree leaf biomass and elevation were significantly correlated ($r = .83$, $P \leq .05$). Otherwise the total leaf biomass in tree- or shrub-dominated plots was not significantly related to the other four site indices.

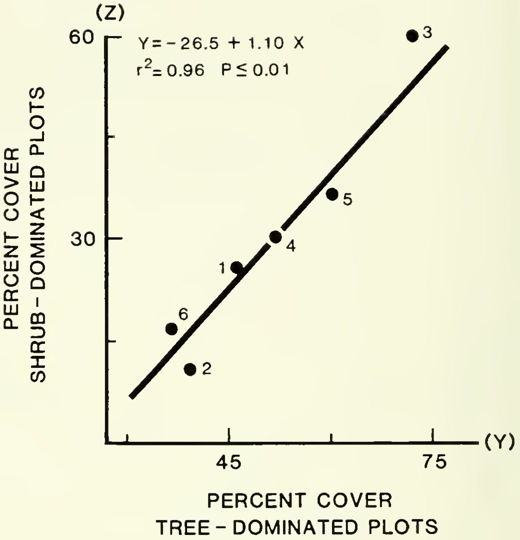

Fig. 3. Regression analysis between the total percentage of vegetal cover in tree-dominated plots and shrub-dominated plots over six sites. Axis designations follow those in Figure 1. Site numbers follow Table 1.

The slope of the line in Figure 5 is deceptive because the ratio of tree to shrub foliage biomass was not constant between sites. This ratio was significantly negatively correlated with Site Class I (Fig. 6). Total foliage biomass in the shrub-dominated plots increased more with better site conditions (about threefold) than in the tree-dominated plots (about twofold). The slope in Figure 5 reflects both the actual ratio and its increase with higher levels of foliage biomass.

The lack of correlation between total foliage biomass and total percentage cover for tree- and shrub-dominated plots was not the case for individual species. Total foliage biomass of the two most common shrubs (mountain big sagebrush, *Artemisia tridentata vaseyana*, and bitterbrush, *Purshia tridentata*) had significant ($P \leq .01$) correlations ($r = .99$ and $r = .96$) with their respective percentage of cover values. Total foliage biomass of the most common bunchgrass (*Sitanion hystrix*) also significantly correlated ($r = .89$, $P \leq .025$) with its percentage of cover.

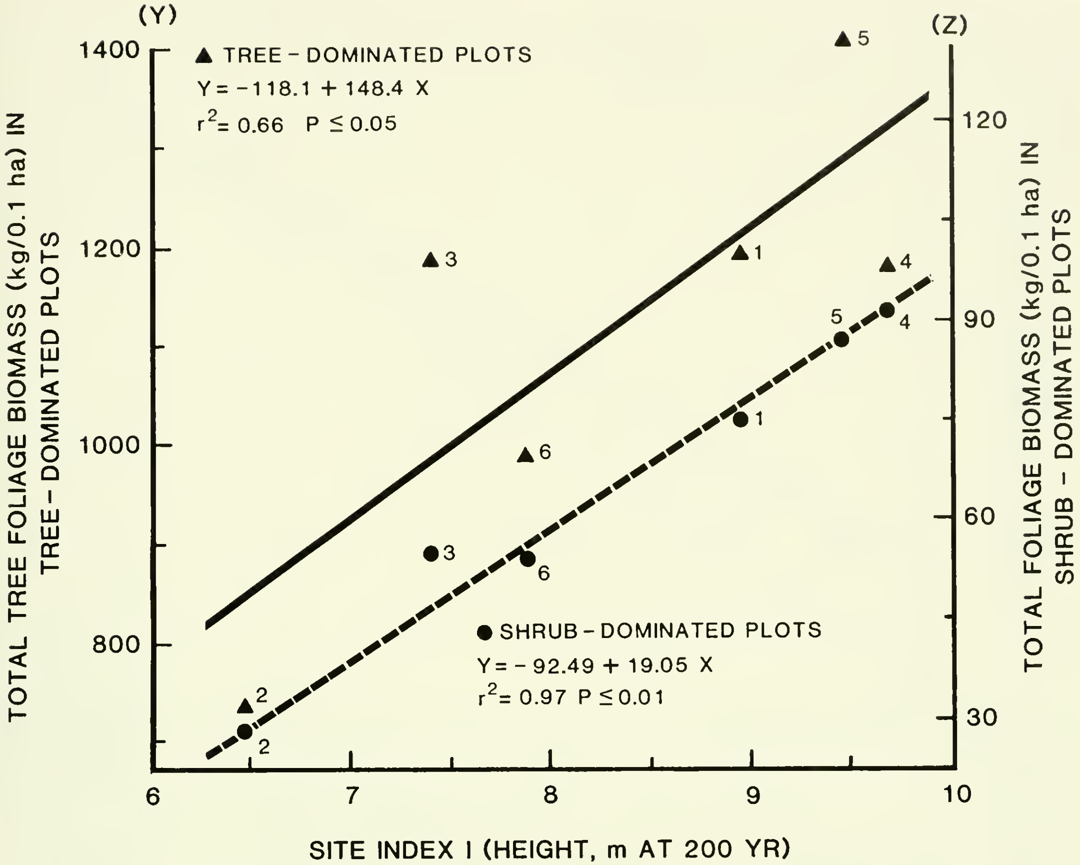

Fig. 4. Regression analyses between Site Index I and total foliage biomass in both tree-dominated plots and shrub-dominated plots. Axis designations follow those in Figure 1. Site numbers follow Table 1.

The number of species sampled in the shrub-dominated plots correlated with both the total foliage biomass in those plots and with Site Index I (Table 5). Species sampled also positively correlated with total foliage biomass of tree-dominated plots (Table 5) and negatively correlated with the foliage biomass ratio ($r = -.86$, $P \leq .05$). But the species sampled were not significantly correlated with the vegetal cover in either the shrub- or tree-dominated plots, with the percentage of cover ratio, or with the other four site indices. A positive relationship occurred between the percentage of cover ratio and total tree foliage biomass ($r^2 = .81$, $P \leq .025$), but not between it and the foliage biomass ratio.

Cheatgrass was negatively correlated with all the other components of the shrub-dominated plots (Table 5). The highest negative correlation for cheatgrass was with the total tree foliage biomass in the paired tree-dominated plots. Tree- and shrub-dominated plots had sufficiently similar environmental conditions for many relationships to exist between them.

A larger effect of topography on foliage biomass than on vegetal cover was evident in the data. Sites 2 and 6 were at nearly the same elevation and less than 200 m apart. Percentage of cover (Fig. 2) did not reflect the environmental differences between a steep north slope (site 6) and a flat alluvial fan surface (site 2). Topography strongly affected both tree and shrub plot foliage biomass data. Foliage biomass on the north slope (site 6) was about one-third more than on the fan (site 2). Differences in species composition may have also affected foliage biomass more than cover.

Sites 3 and 5 are a similar comparison. Site 5, high on the side of the main mountain mass,

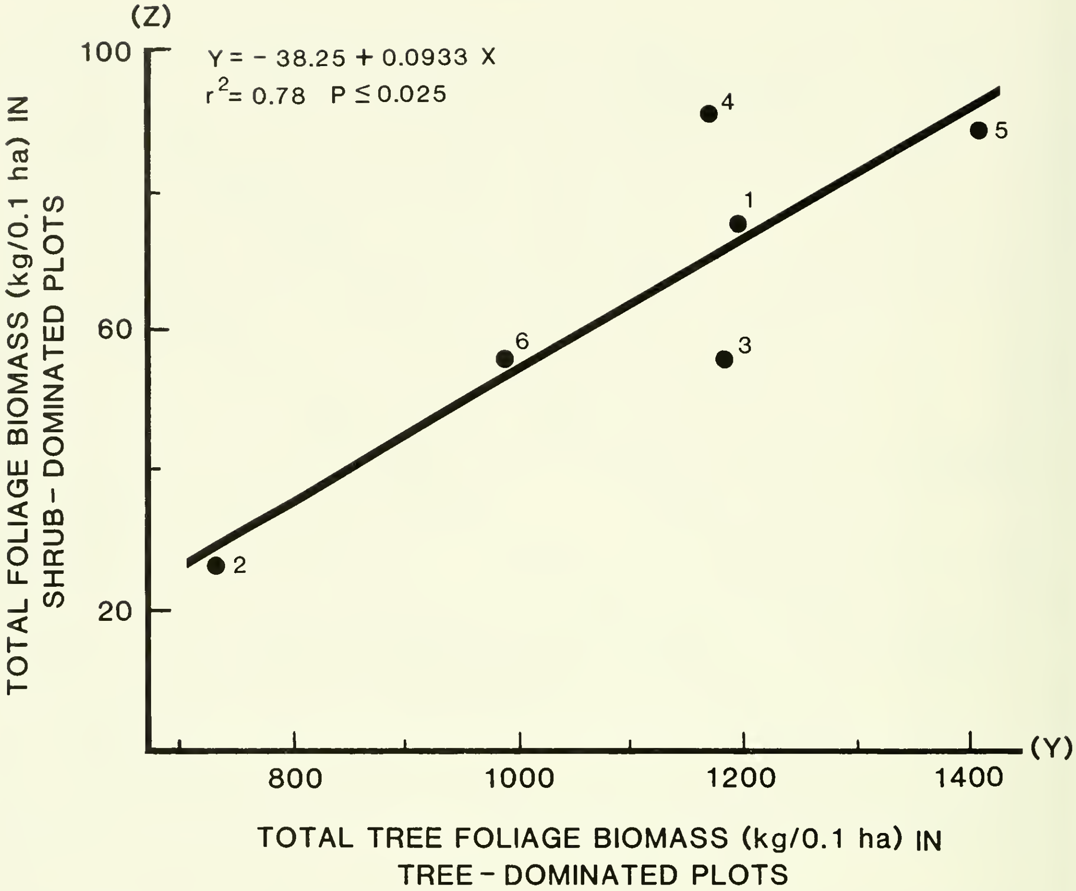

Fig. 5. Regression analysis between the total tree foliage biomass in tree-dominated plots and total foliage biomass in shrub-dominated plots over six sites. Axis designations follow those in Figure 1. Site numbers follow Table 1.

had jeffrey pine (*Pinus jeffreyi*) in the vicinity. Site 3, on top of a foothill, appeared drier but had slightly higher cover (Fig. 2). The higher cover on site 3 appeared to result from a higher density of smaller plants. For total foliage biomass, the situation was reversed, with site 5 about one-third higher than site 3.

The paired tree-dominated and shrub-dominated plots on each site were connected by dashed lines (Fig. 7) to approximate the a–e–e′–a′ successional plane in Figure 1. The site-to-site connections between shrub- and tree-dominated plots were, with one exception, regular over the range of foliage biomass values sampled. At least on the mountain range sampled, the tradeoffs involved are generally consistent with the hypotheses of Figure 1.

Site Index I and elevation did not significantly correlate with each other or with the other three site indices. Site Index II, tallest tree, and average tree height were significantly correlated only with each other (Table 6).

Conclusions

Foliage biomass and percentage of cover variation in both shrub- and tree-dominated communities had significant responses to environmental differences. Responses reflected the hypotheses of Figure 1 but were not the same for foliage biomass or cover. Total foliage biomass in both tree- and shrub-dominated plots was correlated with Site Index I (height at 200 years of age). They also correlated with each other but not with percentage of cover. Percentage of cover correlated best with elevation. Total foliage biomass was more variable in response to topographic differences between sites than total percentage of cover.

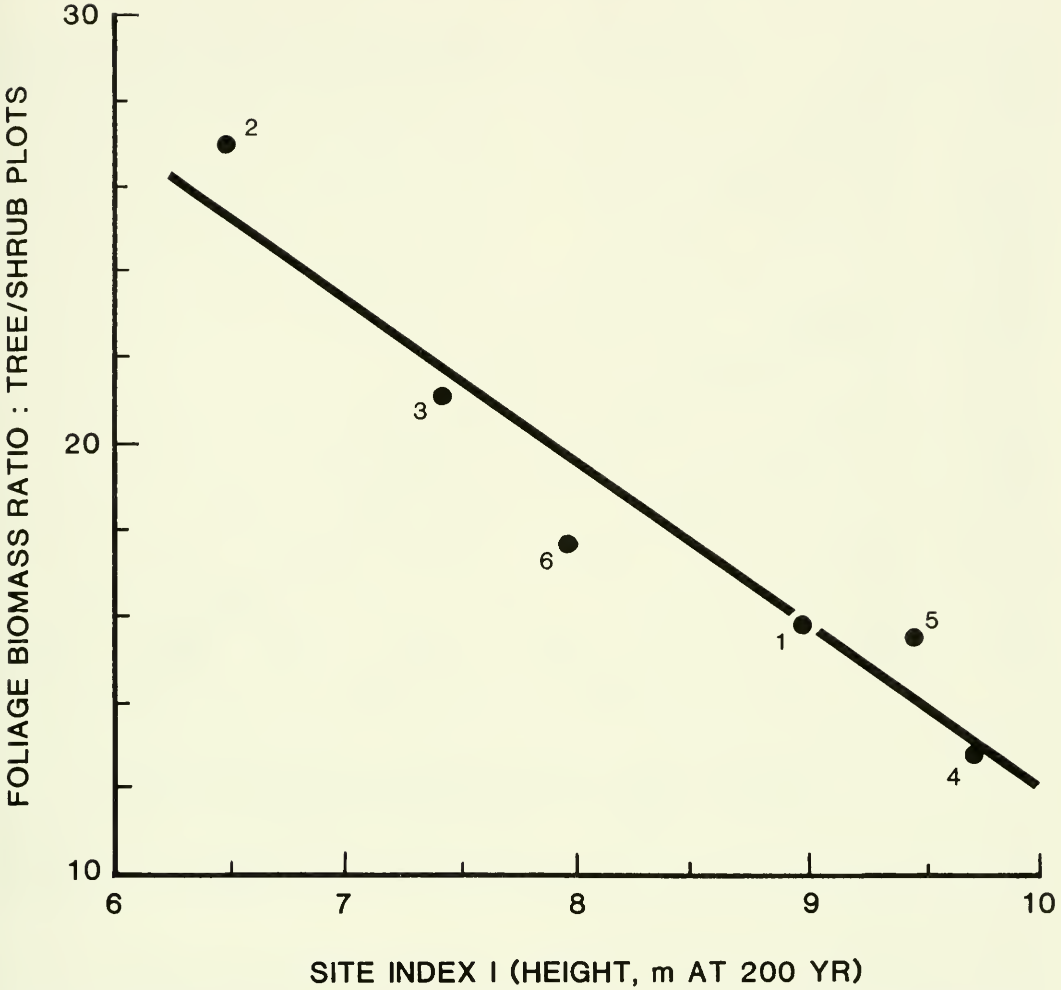

Fig. 6. Regression analysis between the Site Index I values and the ratio of total foliage biomass in tree-dominated plots divided by that in shrub-dominated plots. Site numbers follow Table 1.

TABLE 5. Correlation coefficients between four foliage biomass components and the number of plant species sampled in shrub-dominated plots, among those components and the total foliage biomass in tree- and shrub-dominated plots, and with Site Index I. Relationships between foliage biomass and Site Index I are in Figure 4.

	Total foliage biomass				Species sampled
	Shrub	Perennial grass	Cheatgrass	Forbs	
Shrub	1.00	.34	−.80[a]	.67	.82[b]
Perennial grass		1.00	−.51	.14	.76[a]
Cheatgrass			1.00	−.49	−.72
Forbs				1.00	.66
Species sampled					1.00
Total foliage biomass (tree-dominated plots)	.79[a]	.74[a]	−.87[a]	.28	.81[b]
Total foliage biomass (shrub-dominated plots)	.95[c]	.60	−.79[a]	.59	.94[c]
Site Index I	.92[c]	.60	−.71	.66	.96[c]

[a] $P \leq .10$.
[b] $P \leq .05$.
[c] $P \leq .01$

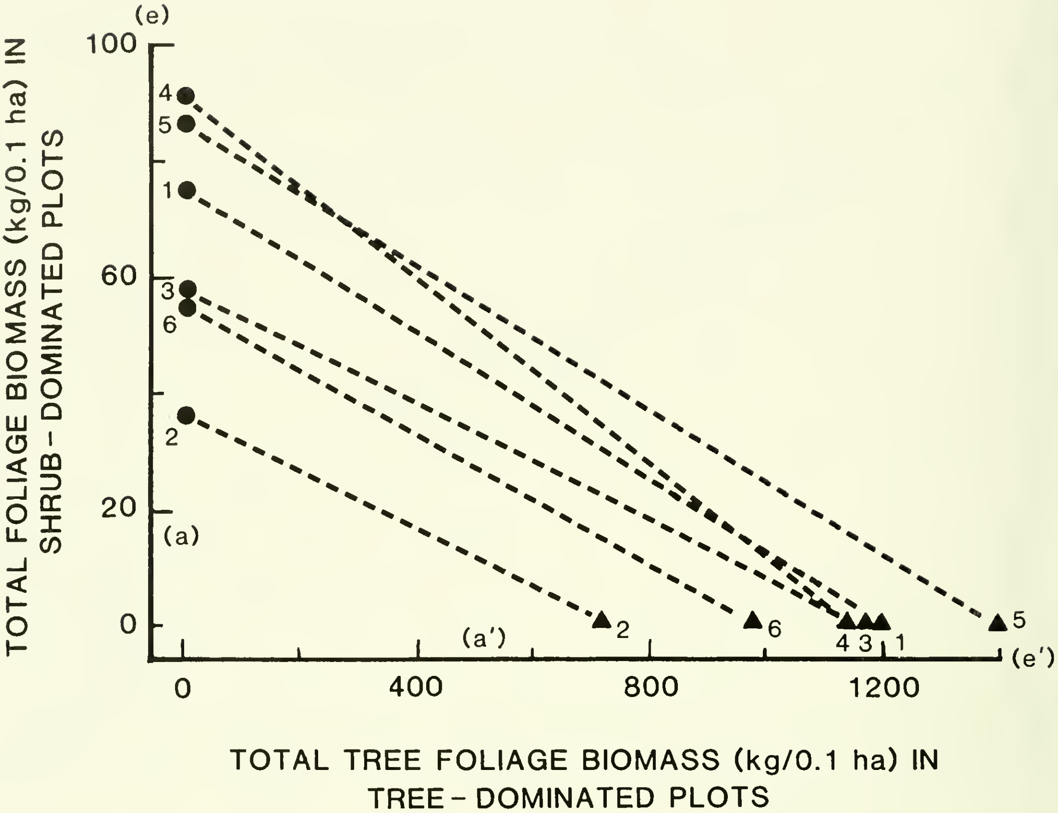

Fig. 7. Comparisons of the relationships between total foliage biomass of tree- and shrub-dominated plots on six sites on the Sweetwater Mountains. Axis designations follow those in Figure 1. Site numbers follow Table 1.

Table 6. Correlation coefficients among three site indices of tree height at 25.4 cm basal diameter (Site Index II), the height of the tallest tree, and the average height of dominant and co-dominant trees in six tree-dominated plots.

	Site Index II	Tallest tree	Average tree height
Site Index II	1.00	.97[b]	.91[a]
Tallest tree		1.00	.95[b]
Average tree height			1.00

[a] $P \leq .05$.
[b] $P \leq .01$

Foliage biomass is also closely related to primary production (Whittaker and Niering 1975) and would appear to be a more sensitive measure for monitoring management results.

Foliage biomass and vegetal cover represented different indicators of environmental variation among sites. This appears to be related to the considerable size/density variation among individual plants and species possible when two or more sites are compared. A community of many small plants and/or many small species has higher vegetal cover than a community with the same total foliage biomass but with fewer, larger plants (Tausch 1980).

Foliage biomass on tree-dominated plots was about 12–25 times higher than on shrub-dominated plots (Fig. 6). This difference may be related to a more efficient use of site resources by the trees (Doughty 1987). Foliage biomass ratios also had inverse relationships to both total foliage biomass and increasing elevation. Total leaf biomass, and possibly annual productivity, in shrub-dominated communities increases more with better site conditions than in tree-dominated communities. The primary resource involved with improving site conditions appears to be moisture availability, as described by Nemani and Running (1989).

Our foliage biomass data for shrub- and tree-dominated communities are from only six sites on one mountain range. They do not fully represent the range of variation present on that mountain range. In many areas of this and other mountain ranges the species composition of the tree- and shrub-dominated sites can have large variations from the sites used here. Specific foliage biomass levels and ratios could thus differ for other sites. Additional studies, particularly on a regional basis, will be needed to better establish the variation in the foliage biomass levels and ratios involved.

Height versus age curves, widely used in commercial forestry, appear to be useful in determining site class on Great Basin sites with pinyon, at least in the Sweetwater Mountains. For our data this site index most closely correlated with total foliage biomass and, therefore, potentially with primary production. A height versus age site index also appears to work equally well for both tree- and adjacent shrub-dominated communities on the same sites. An available index for site could potentially increase ease and accuracy of determining site potential for management of shrub-dominated communities, particularly in association with pinyon-juniper woodlands. Additional verification is required to determine the suitability of a site index method for this and other areas of the Great Basin.

ACKNOWLEDGMENTS

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TAXONOMY AND VARIATION OF THE *LOPIDEA NIGRIDIA* COMPLEX OF WESTERN NORTH AMERICA (HETEROPTERA: MIRIDAE: ORTHOTYLINAE)

Adam Asquith[1]

ABSTRACT.—External morphological variation in the *Lopidea nigridia* "complex" of western North America was examined using principal component analysis and showed continuous variation among populations in most characters. External morphology did not parallel paramere structure and did not substantiate previously recognized species. There was little correlation between dorsal coloration and paramere structure. Cluster analysis (UPGMA) using paramere and color characters failed to group populations coded as the same species and also failed to group all specimens of any one population. The variation in structure of the parameres and vesicae among populations of the *nigridia* complex was no greater than the interpopulational variation of these structures in the congeneric species *marginata* Uhler.

Lopidea nigridia Uhler is treated as a polytypic species comprising three subspecies: *Lopidea nigridia nigridia* Uhler, a fuscous-white form from the sagebrush steppe of the Great Basin and the chaparral of southern California; *Lopidea nigridia serica* Knight, a solid red form from the eastern slopes of the Rocky Mountains from Alberta to Colorado and east across the northern Great Plains to southern Manitoba; *Lopidea nigridia aculeata* Van Duzee, a polymorphic form varying from solid red to fuscous red and white from the Cascade Mountains and eastern slopes of the coastal ranges of British Columbia, Washington, and Oregon, the Blue and Wallawa mountains of Oregon and Washington, and throughout the Coastal and Sierra Nevada ranges of California.

The following new synonymies are created: *Lopidea nigridia nigridia* Uhler = *Lopidea raineri* Knight, *Lopidea sculleni* Knight, *Lopidea rolfsi* Knight, and *Lopidea wilcoxi* Knight; *Lopidea nigridia aculeata* Van Duzee = *Lopidea nigridea hirta* Van Duzee, *Lopidea usingeri* Van Duzee, *Lopidea discreta* Van Duzee, *Lopidea fallax* Knight, *Lopidea yakima* Knight, *Lopidea audeni* Knight, *Lopidea eriogoni* Knight, *Lopidea calcaria Knight*, *Lopidea chamberlini* Knight, *Lopidea angustata* Knight, *Lopidea rubrofusca* Knight, and *Lopidea flavicostata* Knight and Schaffner; *Lopidea nigridia serica* Knight = *Lopidea medleri* Akingbohungbe.

Lopidea Uhler comprises over 100 described species from Central and North America (Henry and Wheeler 1988). Most are large (>5.0 mm), brightly colored plant bugs displaying some pattern of contrasting red-black or yellow-black coloration. There is no taxonomic revision of the genus, but most species were described in a series of papers by Knight (1917, 1918a, 1918b, 1923, 1962, 1965) and Knight and Schaffner (1968, 1972).

Many species are superficially very similar in habitus, and most have been distinguished by the form of the right paramere. This structure is relatively uniform in any given species but extremely variable in size and form among different species of *Lopidea*. It appears that this is the most valuable diagnostic character available for distinguishing different species of *Lopidea*, aside from the vesica.

External and internal male genitalia are now widely used to differentiate taxa in certain groups of Heteroptera, but detailed studies of the variation in these structures are lacking. In the Orthotylini, males often have elaborate parameres and vesicae, and differences in these structures are used to define species (Kelton 1959, Stonedahl and Schwartz 1986). The limits of the variation of these structures in populations and throughout the range of species need to be defined.

Several species of *Lopidea* described from western North America have parameres very similar if not identical to an earlier described species, *Lopidea nigridia* Uhler. I undertook the present study to resolve the taxonomy of this group, which I refer to as the *nigridia* "complex." In this paper I describe the morphological, genitalic, and color variation within this complex and document the characters that unite it as a single taxonomic unit.

MATERIAL AND METHODS

Over 3,000 specimens from throughout the range of *Lopidea* were examined during the course of this study. Male specimens with

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"*nigridia* type" paramere morphology and the associated females were sorted by grouping series that displayed common patterns of color, size, and paramere morphology. Locality data from all specimens examined are available in the author's doctoral dissertation, Oregon State University.

Male genitalia of specimens from different geographic localities within each group were examined. Techniques for the dissections generally followed Kelton (1959). To determine the infraspecific variation in the structures, I compared variation within and among the populations with the closely related species *marginata* Uhler. I had previously determined that the female genitalia are too uniform throughout the genus to provide information at the specific and subspecific levels.

Morphological variation in this complex was examined by recording metric data from 139 males from the following localities (*N* follows each locality): Mexico: Baja California Norte, Parque San Pedro (7); California: Los Angeles Co., El Segundo (10); Mono Co., Leavitt Meadow (10); Trinity Co., Buckhorn Mt. (14); Tuolumne Co., Yosemite Park (10); Colorado: Elbert Co., Kiowa (11); Nevada: Elko Co., (7); Oregon: Polk Co., Dallas (2); Crook Co., Ochoco Summit (10); Deschutes Co., Metolius River (5); Harney Co., Pike Creek (5); Jackson Co., Pinehurst (10); Washington: Pierce Co., Mt. Adams (10); Pierce Co., Mt. Rainier (10); Wyoming: Carbon Co. (14).

Specimens from Mt. Adams and Mt. Rainier are topotypes of *L. rolfsi* Knight and *rainieri* Knight, respectively. Samples from the rest of the populations were selected to cover the range of type localities as well as color and paramere variation of the nominal species in the *nigridia* complex.

Table 1. Correlations between the first two principal components and the morphometric measurements of male *Lopidea nigridia*.

Character	PC I	PC II
Rostral length	0.636	−0.731
Hind tibial length	0.896	0.129
Antennal segment 1	0.912	0.173
Antennal segment 2	0.870	0.288
Head width	0.892	−0.135
Pronotal length	0.941	0.032
Anterior pronotal width	0.847	0.002
Posterior pronotal width	0.892	−0.031

An ocular micrometer was used to measure eight external characters: rostral length (RL) (because the rostrum was often bent at the joints, making its total length difficult to ascertain, only the length of the last three segments was measured); hind tibial length (HTL); length of antennal segment 1 (A1); length of antennal segment 2 (A2); width of head across eyes (HW); maximum length of the pronotum (PL); anterior width of the pronotum (APW); posterior width of the pronotum (PPW). To examine the multidimensional morphological variation in these populations, I applied principal component analysis to the measurements (PCA; Morrison 1976) using SYSTAT (Wilkinson 1986). Although a logarithmic transformation usually results in a more nearly normal distribution of the data (Sokal and Rohlf 1981), it can also distort the multivariate space described by the measurements (Ricklefs and Travis 1980). Analyses using both raw and log-transformed data produced almost identical results; therefore, only results using raw data are presented here.

Because most of the described species in the *nigridia* complex were based on differences in color and male paramere morphology, I recorded eight characters of color and paramere morphology from the 139 specimens used in the morphometric analysis. Color characters were calli, scutellum, embolium, and cuneus, and they were coded for black, red, or white. Paramere characters included angle of the dorsal spine (CA), straight, slightly angled, acute; number of serrations on apex of paramere (SER); number of spines/bifurcations at apex of dorsal spine (SPIN); development of secondary spine on body of paramere (SECSPIN). These data were standardized and analyzed by SPSS/PC Hierarchical Cluster Analysis using UPGMA on distance matrices of squared euclidean distances.

Results

Principal Component Analysis

The first two principal components accounted for 84% of the morphological variation among individuals. The first component (PC I, 76.1%) reflects the general size variation among individuals; all variables were positively correlated with PC I (Table 1). PC II

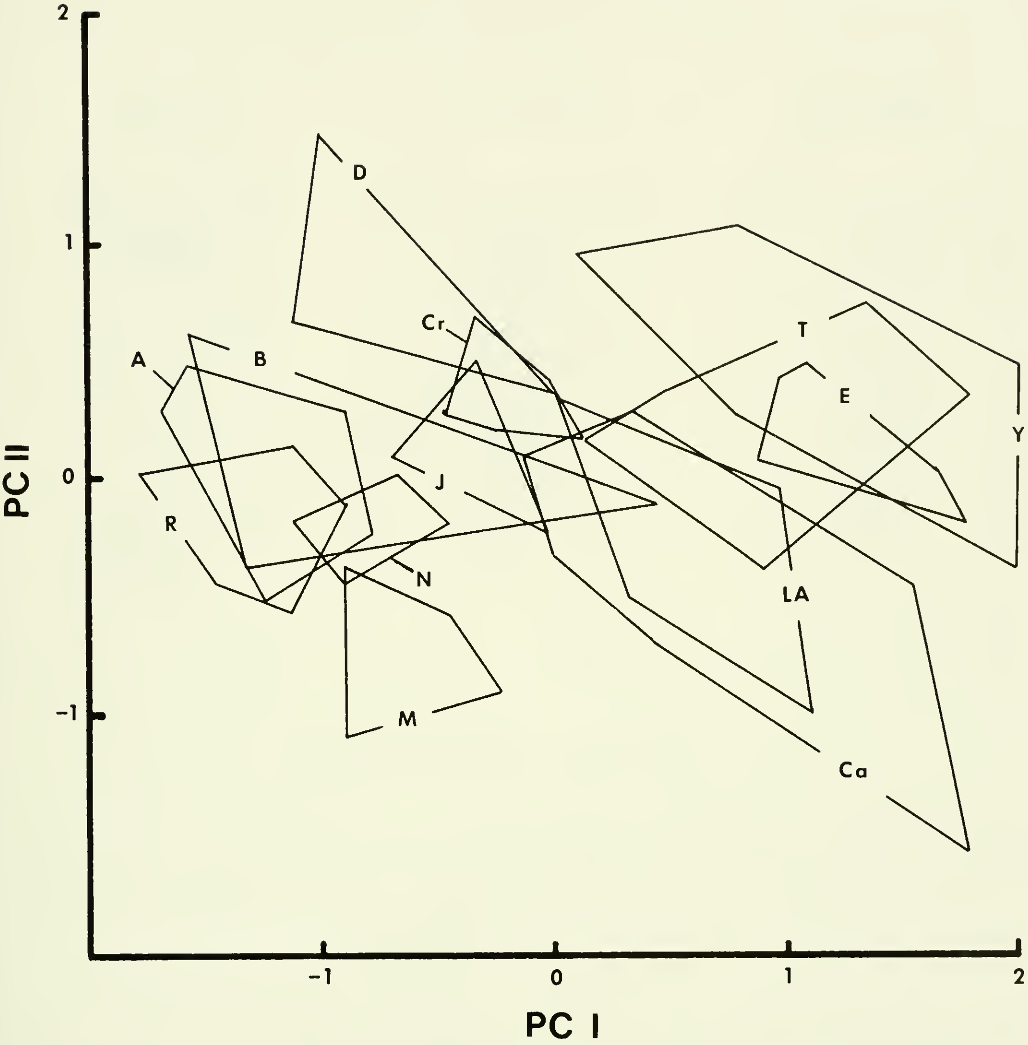


Fig. 1. Morphological variation of *Lopidea nigridia* Uhler based on principal component analysis. Populations are plotted on the first (PC I) and second (PC II) principal components, enclosed in polygons connecting the outlying individuals of each sample. Abbreviations: R = Mt. Rainier, WA (*L. n. nigridia*); A = Mt. Adams, WA (*L. n. nigridia*); Ca = Carbon Co., WY (*L. n. serica*); N = Elko Co., NV (*L. n. nigridia*); B = Baja California Norte (*L. n. aculeata*); J = Jackson Co., OR (*L. n. aculeata*); Cr = Crook Co., OR (*L. n. aculeata*); LA = Los Angeles Co., CA (*L. n. nigridia*); M = Mono Co., CA (*L. n. nigridia*); E = Elbert Co., CO (*L. n. serica*); T = Trinity Co., CA (*L. n. aculeata*); Y = Yosemite Park, CA (*L. n. aculeata*); D = Deschutes Co., OR (*L. n. aculeata*).

(7.9%) reflects an inverse relationship between RL and A2. To illustrate the distribution of populations in the morphological space described by the principal components, individuals were plotted on axes described by PC I and PC II and populations were enclosed in polygons by connecting the outlying individuals with lines (Fig. 1).

This analysis illustrates some of the morphological differences among populations. For example, the Yosemite population (Y) is composed of large individuals with relatively long antennae and short rostra. The Mono County population (M) is composed of relatively small individuals with short antennae and long rostra. These two populations examined separately are quite distinct; they do not overlap in overall size and have differently proportioned antennae and rostra. However, both populations overlap other groups to

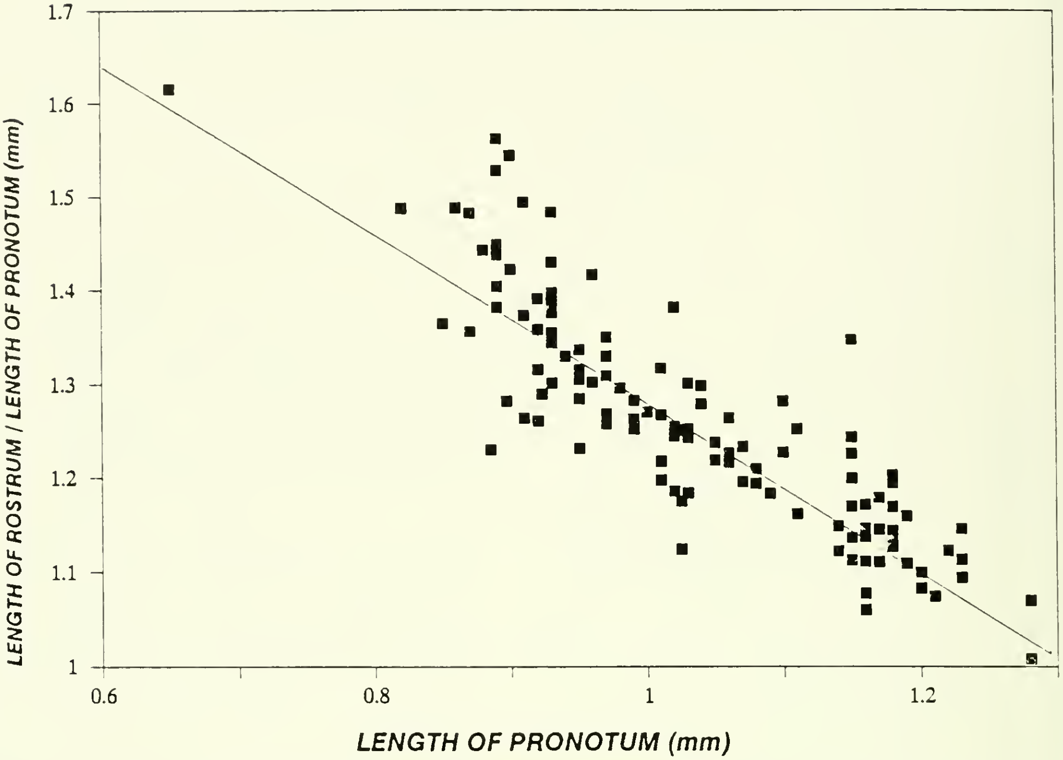


Fig. 2. Relationship between relative length of the rostrum (rostrum length/pronotum length) and pronotum length in *Lopidea nigridia*; $y = 2.1777 - 0.884x$, $r^2 = 0.757$, $N = 128$.

some degree, creating a continuum of morphological variation in all dimensions. This pattern makes it difficult to clearly segregate a population or groups of populations based on external morphology alone.

There was no clear pattern of morphological variation with regard to geography. The largest individuals were found in two California populations (Y, T), the Wyoming population (Ca), and the Colorado population (E). Individuals with short antennae and long rostra were found in the Wyoming population (Ca) and a California population (M). The two most morphologically similar populations were Wyoming (Ca) and Los Angeles County (LA).

Not all coefficients of variables in the PCA analysis were of equal magnitude, suggesting allometric relationships among the variables. For example, PC I represents general size variation among individuals, and rostral length has the lowest correlation with PC I (Table 1). This suggests that as size increases rostral length increases more slowly than other characters.

The significance of this pattern can be seen by examining the relationship of rostral length to the best single measure of size, pronotal length. The relative length of the rostrum (RL/PL) decreases with increasing size (Fig. 2). Very small individuals have rostra that are 1.5 times the length of the pronotum, whereas very large individuals have rostra that are only equal to the length of the pronotum. This has important implications regarding the taxonomic value of these and similar characters, such as the distance the rostrum extends posteriorly on the sternum. In very small individuals of the *nigridia* complex the rostrum extends to or slightly beyond the metacoxae, whereas in large individuals the rostrum may not reach the mesocoxae.

Color Pattern

Dorsal coloration of individuals from any one series was usually uniform, but color

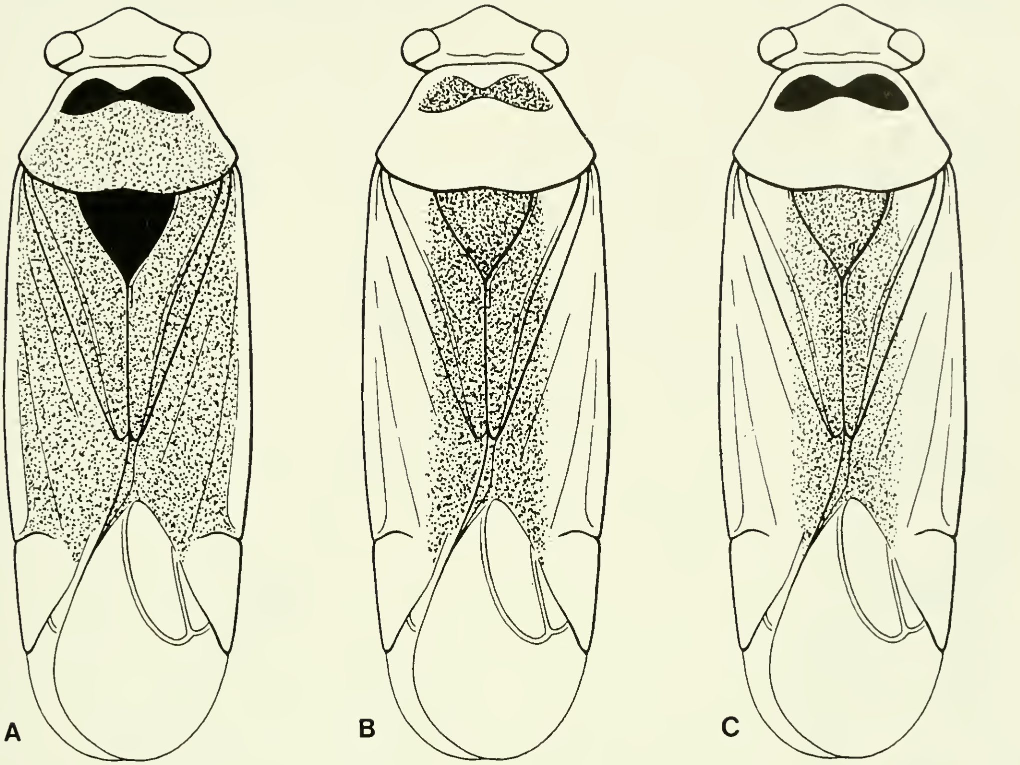


Fig. 3. Variation in dorsal color pattern of *Lopidea nigridia* Uhler: A, fuscous-white color pattern characteristic of *L. n. nigridia* Uhler; B, fuscous-red-white color pattern characteristic of *L. n. aculeata* Van Duzee; C, solid red color pattern characteristic of *L. n. serica* Knight. Stippled areas represent fuscous coloration; gray areas represent red coloration.

varied dramatically among collections. At one extreme is a red form that is uniformly brick red with slight to moderate infuscation on the clavus. At the other extreme is a fuscous-white form with the clavus and corium predominantly to completely reddish fuscous and the embolium and cuneus pale white (Fig. 3). Color variants intermediate of the two extremes also occur.

The color patterns of the *nigridia* complex also occur in several related sympatric species. *Lopidea marginata* Uhler displays very similar color variation, with some populations composed of solid red individuals, while in other populations the clavus and corium are infuscated and the embolium and cuneus pale white.

The different color forms in the *nigridia* complex do not appear to be segregated with regard to host plant west of the Rocky Mountains, and both color extremes have been collected from near sea level in southern California to >5,000 ft. elevation in the Sierra Nevada and Cascade Mountain ranges. The most conspicuous geographic patterns are the absence of the red form from the Intermountain Sagebrush Province and the absence of the fuscous-white form from the Great Plains short-grass prairie (Fig. 4). This latter pattern also seems to correspond to a switch in preferred host plants from *Lupinus* to *Astragalus* (see Biology).

Paramere Structure

There were few correlations between color and paramere variables and morphology. PC I, representing size, was negatively correlated with the number of serrations on the paramere and all color variables (Table 2). In general, populations of large individuals also

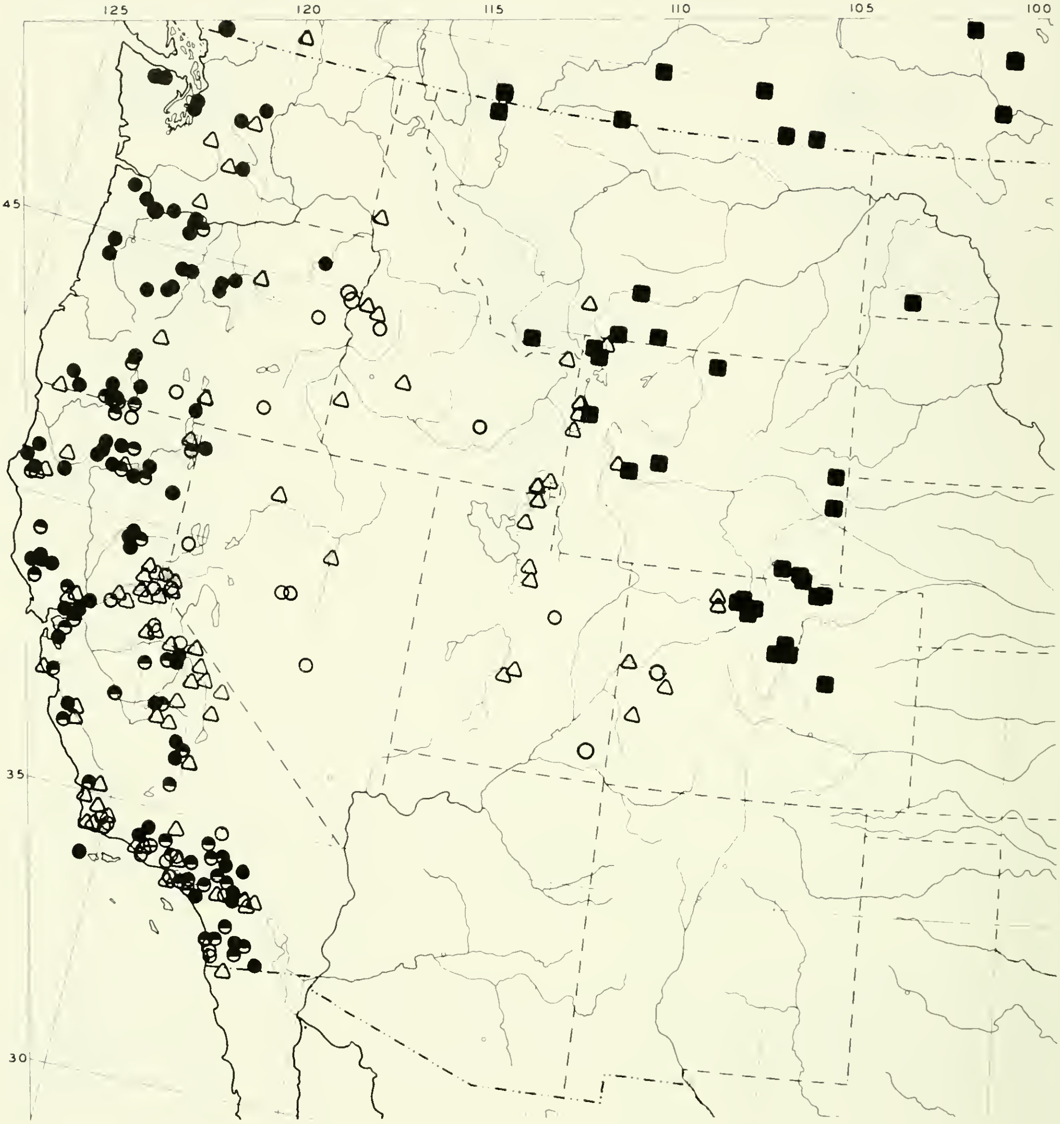


Fig. 4. Distribution of subspecies and color forms of *L. nigridia* Uhler in western North America: triangles = fuscous white form of *L. n. nigridia* Uhler; open circles = more reddish color form of *L. n. nigridia* Uhler; solid circles = solid red color form of *L. n. aculeata* Van Duzee; half solid circles = red-white color form of *L. n. aculeata* Van Duzee; solid squares = *L. n. serica* Knight.

tend to have more serrations and to be solid red with no white on the embolium or cuneus, and smaller individuals have fewer serrations and are more fuscous with a white embolium and cuneus. Although this trend was apparent for most specimens I examined, it was not always true; individuals from Deschutes Co., Oregon (D), are relatively small and yet are solid red in color, and I have seen very large specimens from Santa Barbara Co., California, that have a light embolium and cuneus.

Many characters of the right paramere formerly used to distinguish species within the *nigridia* complex vary among individuals within a population. For example, *wilcoxi* Knight was distinguished from *rainieri* Knight by the absence of a secondary spine in *wilcoxi*. In only two populations examined

TABLE 2. Pearson correlation coefficients between the first two principal components and paramere and color characters of male *Lopidea nigridia*. * = significant at alpha < .05; ** = significant at alpha < .001; NS = not significant (alpha > .05).

Character	PC I	PC II
CA	−0.157 NS	−0.121 NS
SER	−0.361 **	−0.066 NS
SPIN	−0.020 NS	−0.054 NS
SECSPIN	−0.067 NS	−0.110 NS
CALLI	−0.308 **	0.195 *
SCUT	−0.207 *	0.180 *
EMBOL	−0.594 **	0.072 NS
CUN	−0.564 **	0.116 NS

did all individuals either have or completely lack this structure. Some populations in the Siskiyou Mountains of California and Oregon contain individuals with a distinct toothed hook ventrally on the apex, used by Knight (1965) to distinguish *calcaria* Knight and *eriogoni* Knight. Other individuals from the same series lack this structure and display parameres more similar to other described species in the complex. Figure 5 illustrates the extent of variation of the right paramere seen in the *nigridia* complex. The only aspect of the right paramere common to all populations and absent in other species of *Lopidea* is the presence of the elongate dorsal spine at the apex.

Examination of the left paramere and internal genitalia corroborated the patterns seen in the right paramere. The left paramere is structurally less complex than its counterpart and thus shows less variation. The medial flange is digitiform, with its distal end usually slightly clavate and free from the main body of the paramere. The vesica bears a slender, slightly curved ventral spicula, toothed at the apex and with a slight swelling at its midpoint. The dorsal spicula is short, broadly lanceolate, toothed, and slightly curved. The variation in these structures between color forms of the *nigridia* complex is no greater than the infraspecific variation seen in other species. This is illustrated in Figure 6, where genitalic structures of a fuscous-white and a red form of *nigridia*, both from Wyoming, are compared with the same structures from individuals of *marginata* Uhler from Oregon and Baja California. The dorsal spicula is usually shorter and straighter in the fuscous-white color form. The dorsal spicula, however, varies in shape from straight and blunt to curved and evenly pointed (Fig. 7); it also shows considerable variation in other species of *Lopidea*.

Cluster Analysis

This analysis demonstrates the difficulty of separating groups within the *nigridia* complex based on color and paramere characters. In no case were all individuals from one population found to be most similar to each other; at least one individual was always grouped with those from another population. In most cases, individuals from any given population were scattered throughout the dendrogram. For example, the Mt. Adams population (A) had individuals placed in four of the five major clusters (Fig. 8A).

The cluster analysis did not identify groups composed of individuals that I determined as being the same color form. For example, all individuals from Crook Co. (Cr), Trinity (T) (Fig. 8B), and Jackson Co. (J) (Fig. 8A) represent the solid red form; however, Cr specimens were grouped in the uppermost cluster, T specimens in the next lower cluster, and J specimens in the middle three clusters. Similarly, specimens representing the fuscous-white form were also found in all of the major clusters. This analysis further suggests that grouping specimens within the *nigridia* complex based on color and paramere morphology gives equivocal results.

TAXONOMY

All specimens examined in this study clearly belong to a monophyletic group. They are united by the presence of an elongate dorsal spine on the apex of the right paramere; a free, digit-shaped medial flange on the left paramere; and a slender, slightly spindle-shaped ventral spicula. These are derived characters found in no other species of *Lopidea*. In addition, all specimens are believed to be conspecific for the following reasons. Populations or groups of populations cannot be distinguished by combinations of external morphological measurements. Although populations display considerable color variation, color is not highly correlated with external or paramere morphology, and similar color variation is seen in related species. Most characters of the right paramere vary among individuals from any population. Only characters

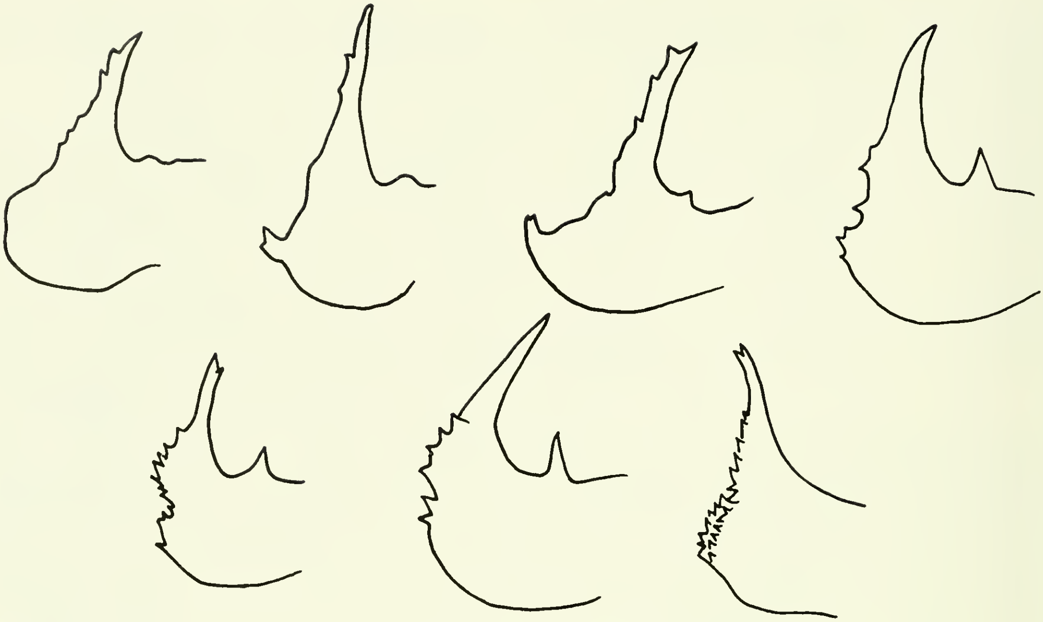


Fig. 5. Variation of right paramere in *Lopidea nigridia* Uhler. Drawn in posterolateral view.

common to all populations, such as the elongated spine on the dorsal apex of the right paramere and the digit-shaped medial flange on the left paramere, also corresponded with unique characters of the male vesica.

I have also examined the type specimens of all nominal species in the *nigridia* complex and have determined, using the above criteria, that they also are conspecific with *nigridia* Uhler. I interpret *nigridia* as being a polytypic species comprising three subspecies segregated to some degree by geography and/or habitat. I have elected to use the subspecies category for these taxa because, based on the available data, it adequately describes the broad geographic patterns of the color forms. I have retained the subspecies *L. n. nigridia* Uhler for the Intermountain, fuscous-white form and *L. n. serica* Knight for the solid red, eastern Rocky Mountain and prairie form. I also recognize *L. n. aculeata* Van Duzee as a polymorphic form of the Pacific Coast states. Below I provide a complete synonymy for *nigridia* and its subspecies. All lectotype and holotype label data are given verbatim.

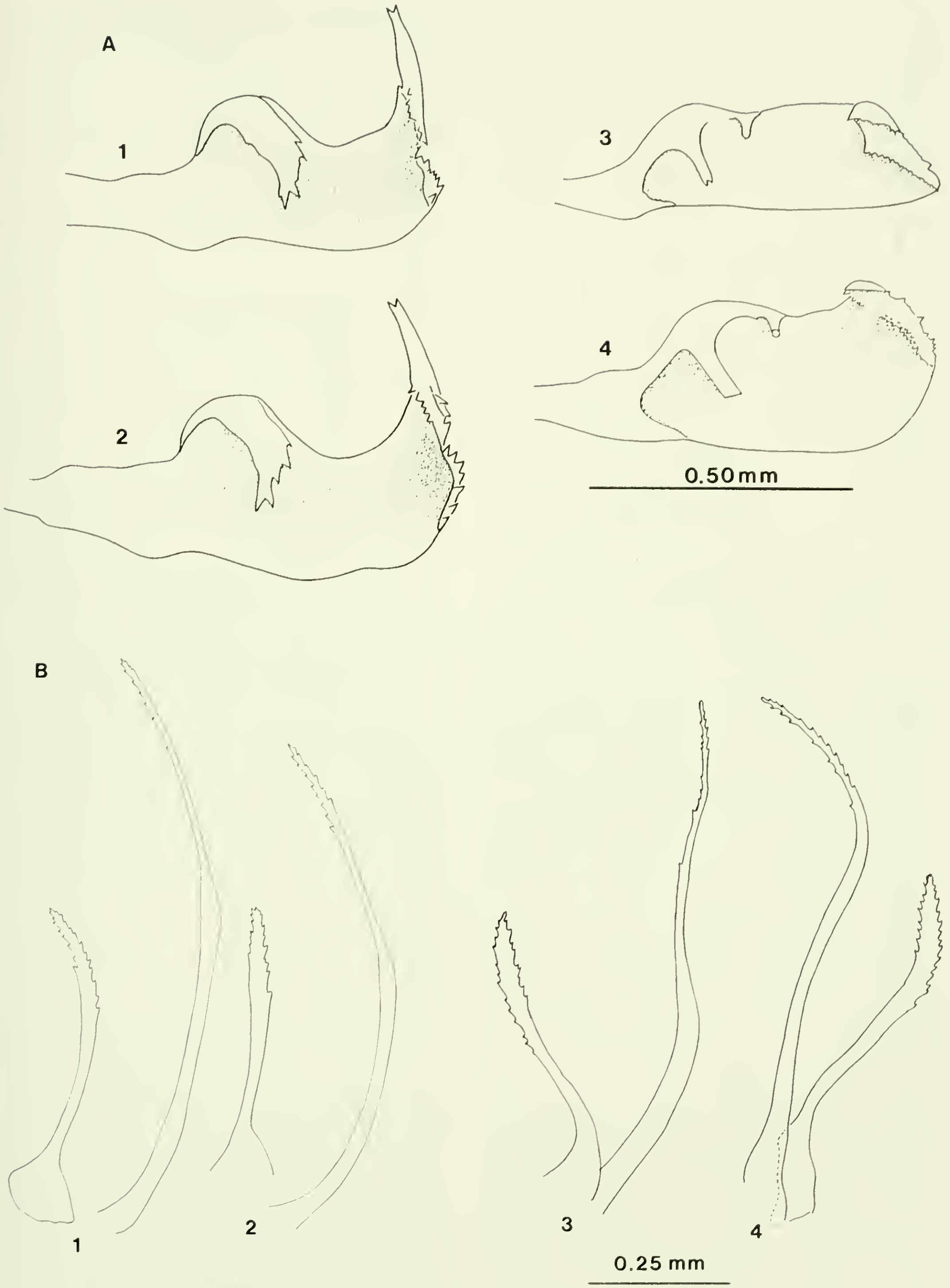
Lopidea nigridia Uhler

Lopidea nigridia Uhler, 1895: 30 (n. sp., desc.).

Lopidea nigridea: Osborn, 1898:233 (dist.). Van Duzee, 1914:28 (list). Van Duzee, 1916:241 (cat.). Van Duzee, 1917:384–385 (cat.). Van Duzee, 1921:127 (n. subsp.). Knight, 1923:69 (fig.). Van Duzee, 1933:96 (note). Carvalho, 1958:87 (cat.). Knight, 1965: 8–10 (fig.). Akingbohungbe, 1972:842 (note). Henry and Wheeler, 1988:422 (cat.).

LECTOTYPE (designated here).—♂, Colo. 1387 [1387 = Steamboat Springs, Col. July C. F. Baker, ex. *Delphinium occidentale*]; *Lopidea nigridea*, det Knight; LECTOTYPE *Lopidea nigridia* Uhler, det A. Asquith; deposited in the USNM.

HOLOTYPES OF SYNONYMS:—*Lopidea aculeata* Van Duzee: ♂, Seattle, Wash.; W. M. Giffard, 7-VII-17; (CAS). *Lopidea angustata* Knight: ♂, Antioch Calif., Sand Dunes, June 4, 1942, H. A. Scullen; (USNM). *Lopidea audeni* Knight: ♂, Midday Valley, Merritt B.C., July 1925, K. F. Auden; (USNM). *Lopidea calcaria* Knight: ♂, Crater Lake, Ore., South Rim, 7100 ft elev., July 29, 1930; H. A. Scullen; (USNM). *Lopidea chamberlini* Knight: ♂, Whitman N. F., OR, VII-22-14; W. J. Chamberlin Collector; (USNM). *Lopidea discreta* Van Duzee: ♂, Huntington Lake Ca., July 26, 19; Fresno Co. 7,000 ft.; E. P. Van Duzee Collector; (CAS). *Lopidea eriogoni* Knight: ♂, Drake Peak, Lake Co., Ore., 7,850 ft. elev., July 26, 1930; (USNM). *Lopidea fallax* Knight: ♂, below Mt. Springs, San Diego Co. Calif., June 11, 1915, Harold



Figs. 6A–B. Comparison of genitalic structures of *Lopidea* species: A, right paramere: 1, *L. n. nigridia* Uhler. Yellowstone Nat. Pk., WY; 2, *L. n. serica* Knight; 3, *L. marginata* Uhler, Benton Co., OR; 4, *L. marginata* Uhler. Baja California Norte. B, Spiculae: species as in A.

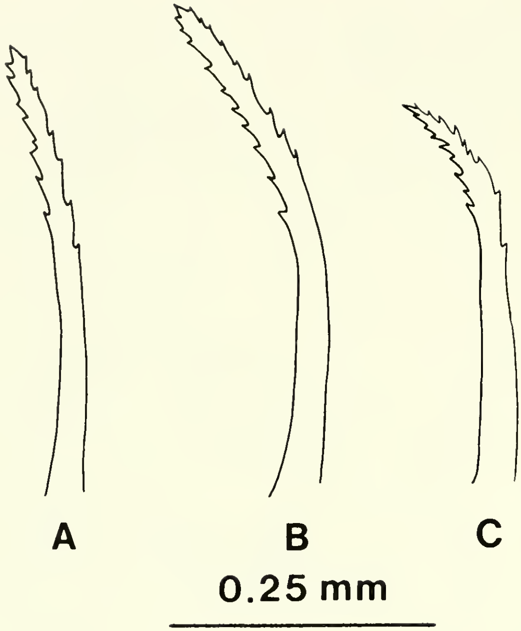


Fig. 7. Variation of the dorsal spicula in *Lopidea nigridia* Uhler: A, *L. n. nigridia* Uhler, Lander Co., NV; B, *L. n. serica* Knight, Carbon Co., WY; C, *L. n. aculeata* Van Duzee, Trinity Co., CA.

Morrison; (USNM). *Lopidea flavicostata* Knight and Schaffner: ♂, Camino, Calif., July 10, 1965, H. H. Knight; (USNM). *Lopidea medleri* Akingbohunge: ♂ (holotype not examined) Eau Claire Co., Fairchild, Wisc., 7-15-63, J. T. Medler (UWM). *Lopidea nigridea hirta* Van Duzee: ♂, San Miguel Isl., Cal., V-20-1919; EP Van Duzee Collector; (CAS). *Lopidea rainieri* Knight: ♂, Mt. Rainier, Wash., Aug. 14, 1931, H. H. Knight; (USNM). *Lopidea rolfsi* Knight: ♂, Mt. Adams Wa., Aug. 3 1930, A. R. Rolfs; (USNM). *Lopidea rubrofusca* Knight: ♂, Monticello, Ut., 6-18-33; G. F. Knowlton Collector [the name written on the holotype label is spelled "*rubrofuscata*" but was published as *rubrofusca*] (USNM). *Lopidea scullei* Knight: ♂, Cornucopia, OR, 7,100′, July 25, 1936, H. A. Scullen, col.; (USNM). *Lopidea serica* Knight: ♂, Ft. Collins, Col. 6-28-00; (USNM). *Lopidea usingeri* Van Duzee: ♂, Oakland Rec. Camp, Cal., VII-20-27; Toulumne Co.; R. L. Usinger Collector; (CAS). *Lopidea wilcoxi* Knight: ♂, Mt. Rainier, Wa., VII-13-'31, sunrise, 6,318′; J. Wilcox, Coll.; (USNM). *Lopidea yakima* Knight: ♂, Olympia, Wash., Aug. '93; (USNM).

DIAGNOSIS.—*Lopidea nigridia* belongs to a western species group united by the rectangular shape and serrate apex of the right paramere; slender, unforked ventral spicula and red-white dorsal color pattern. Males can be distinguished by the presence of a straight, elongate dorsal spine at the apex of the right paramere (Fig. 5).

Because of the common patterns of color variation between *nigridia* and sympatric species, females are difficult to identify. Females of *ute* Knight and *garryae* Knight lack erect, dark setae on the head and pronotum. In *taurina* Van Duzee the dark setae are much shorter and decumbent, and the embolium usually supports only pale setae. Females of *dakota* Knight have the second antennal segment strongly tapered distally. *L. chelifer* Knight is also solid red in eastern Colorado but has the anterior width of the pronotum narrower than *n. serica*, and western populations have white on the clavus. *L. marginata* Uhler can be distinguished only by its smaller size in areas of sympatry and white coloration on the clavus when present.

DISTRIBUTION.—*L. nigridia* is widely distributed throughout western North America, and the three subspecies display a largely parapatric distribution (Fig. 9). In the original description, Uhler (1895) listed this species from New Mexico and Arizona, states in which *nigridia* is not known to occur. Osborn (1898) reported *nigridia* from Iowa. This was clearly a misidentification, as at that time only the fuscous-white *n. nigridia* subspecies was recognized, and this form does not occur east of the Rocky Mountains.

REDESCRIPTION (Male).—Length 4.52–6.55; red to grayish fuscous; dorsum with erect, black setae and small, appressed sericeous setae. HEAD: width across eyes 1.01–1.29, vertex 0.61–0.76, vertically declivent, triangular; tylus produced, arcuate anteriorly, black; distance between antennal fossa and anterior margin of eye less than width of second antennal segment, antennal socket ringed in black; gena red; all sutures black; frons slightly convex, red, vittae black; vertex slightly concave, posterior margin black; basal carina usually distinct, lined with erect, black setae; posterior margin of head straight in dorsal view, postocular regions pale to rufous. ROSTRUM: length 1.53–1.78, black, dorsal surface slightly lighter; first segment rufous or pale dorsally and laterally, reddish fuscous distally with black apex. ANTENNAE: black, fuscous, or red; I, length 0.40–0.64, with two large, stiff setae distally on the medial surface; II, 1.34–2.28; III, 0.81–1.50; IV, 0.35–0.51. PRONOTUM: length 0.65–1.29, posterior width 1.25–1.96, broadly convex, surface smooth, anterior angles rounded, lateral margins carinate, slightly arcuate in dorsal view, lined with erect, black setae, posterior margin straight or slightly sinuate; calli lightly infuscate to piceous, posterior angles broadly rounded, surrounded by fulvus or yellowish white; disc brick red to gray fuscous; propleura smooth, glabrous, episternum fulvus to white, sternum black. LEGS: black, testaceous, or fulvus; coxae and trochanters pale or fulvus; femora black on dorsum, paler on anterior and ventral surfaces, often spotted with fuscous, pale at apex; tibiae black or dark red, tarsi black. GENITALIA: *Tergal process:* relatively long compared with other species of *Lopidea*, evenly narrowed to a sharp point, slightly curved medially. *Right paramere:* roughly rhomboidal in outline, apex with long, erect spine; spine pointed or bifurcate at tip, straight or inclined toward base of paramere (Fig. 5). Apical edge of paramere slightly curved medially, usually with two vertical rows of small teeth; number and position of teeth variable. Small secondary spine occasionally present on dorsal edge near base of apical spine. Basal arm long, thick, curved medioventrally, apex variable, usually bifurcate (Fig. 6). *Left paramere:* sharply angled with apical lobe oval in lateral view. Medial flange distinct, separate from lateral flange for most of its length; narrow, elongate with distal end usually slightly expanded. VESICA: *Dorsal spicula:* short, lanceolate, straight or slightly curved, both margins of distal third serrate (Fig. 7). *Ventral spicula:* long, slender, slightly curved, a small swelling present near middle, apex with small teeth (Fig. 6). VESTITURE: head and pronotum with short, stiff, erect, black setae, black setae on hemelytra variable in length, suberect to erect, occasionally pale on light-colored area of corium, pronotum and hemelytra also with flattened sericeous setae, venter moderately covered with short, suberect pale setae.

FEMALE.—Similar in structure, color, and vestiture, but larger, broader, and more robust; frons more protuberant and broadly convex than in male, vertex flat, basal carina less distinct, lateral margins of pronotum less carinate, hemelytra arcuate laterally. Length 4.82–7.46. HEAD: width across eyes 1.12–1.30, vertex 0.69–0.82. ROSTRUM: length 1.22–1.55. ANTENNAE: I, length 0.51–0.76; II, 1.48–2.49; III, 1.01–1.47; IV, 0.41–0.52. PRONOTUM: length 0.91–1.50, posterior width 1.42–2.17.

Lopidea nigridia nigridia Uhler

Lopidea nigridia Uhler, 1895:30 (n. sp., desc.).

Lopidea nigridea nigridea: Van Duzee, 1921:128. Henry and Wheeler, 1988:423 (cat.).

Lopidea rainieri Knight, 1965:8–9 (n. sp.). Henry and Wheeler, 1988:423 (cat.). *New synonymy*

Lopidea sculleni Knight, 1965:9 (n. sp.). Henry and Wheeler, 1988:424 (cat.). *New synonymy*

Lopidea rolfsi Knight, 1965:9 (n. sp.); Akingbohungbe, 1972:842 (note). Henry and Wheeler, 1988:424 (cat.). *New synonymy*

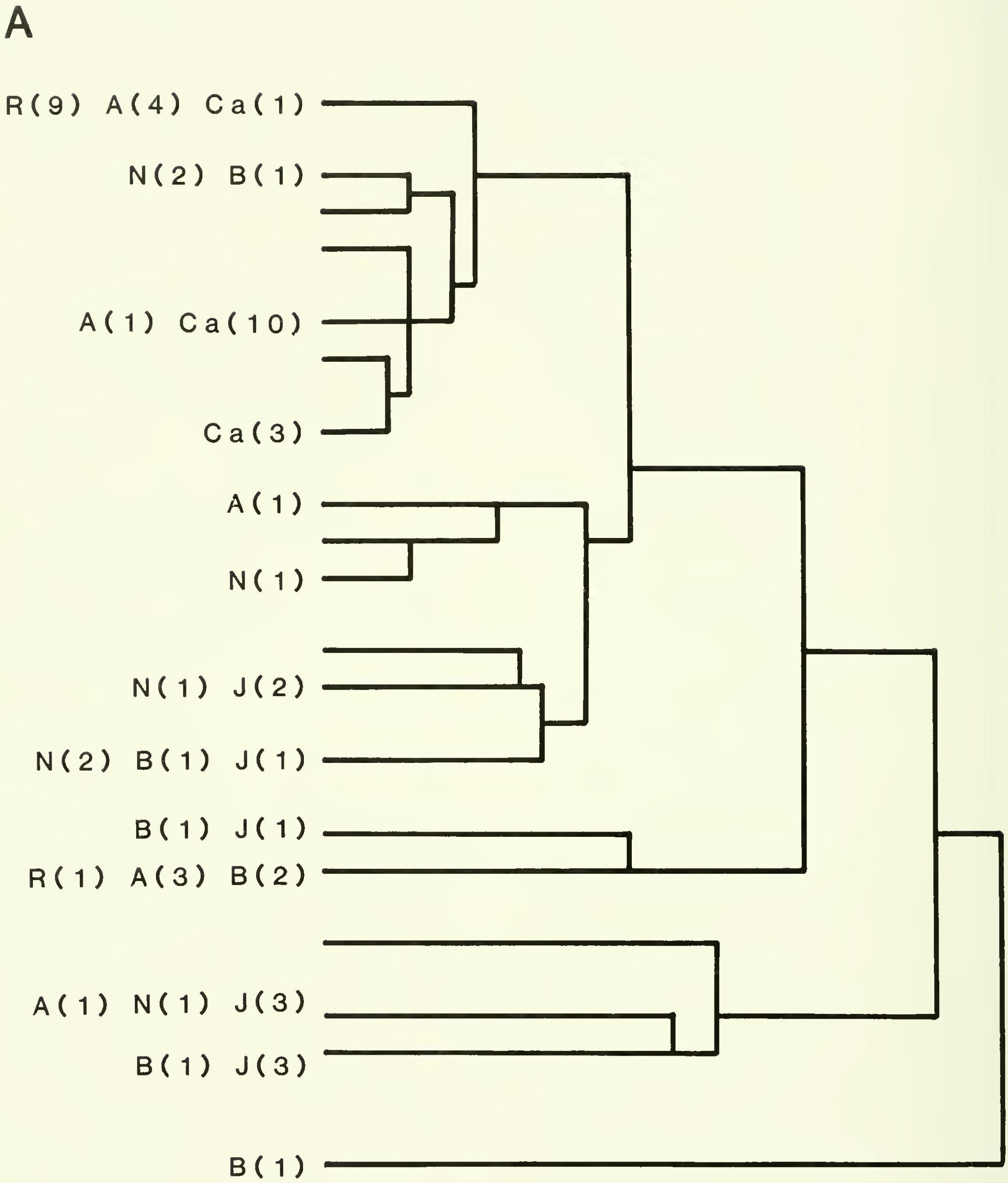
Lopidea wilcoxi Knight, 1965:11–12 (n. sp.). Henry and Wheeler, 1988:425 (cat.). *New synonymy*

DIAGNOSIS.—*L. n. nigridia* Uhler is small to moderate in size, parallel sided, with a contrasting dorsal color pattern of smoky fuscous on the pronotum, scutellum, clavus, and most of the corium and pale white on the outer corium, embolium, and cuneus (Fig. 3A).

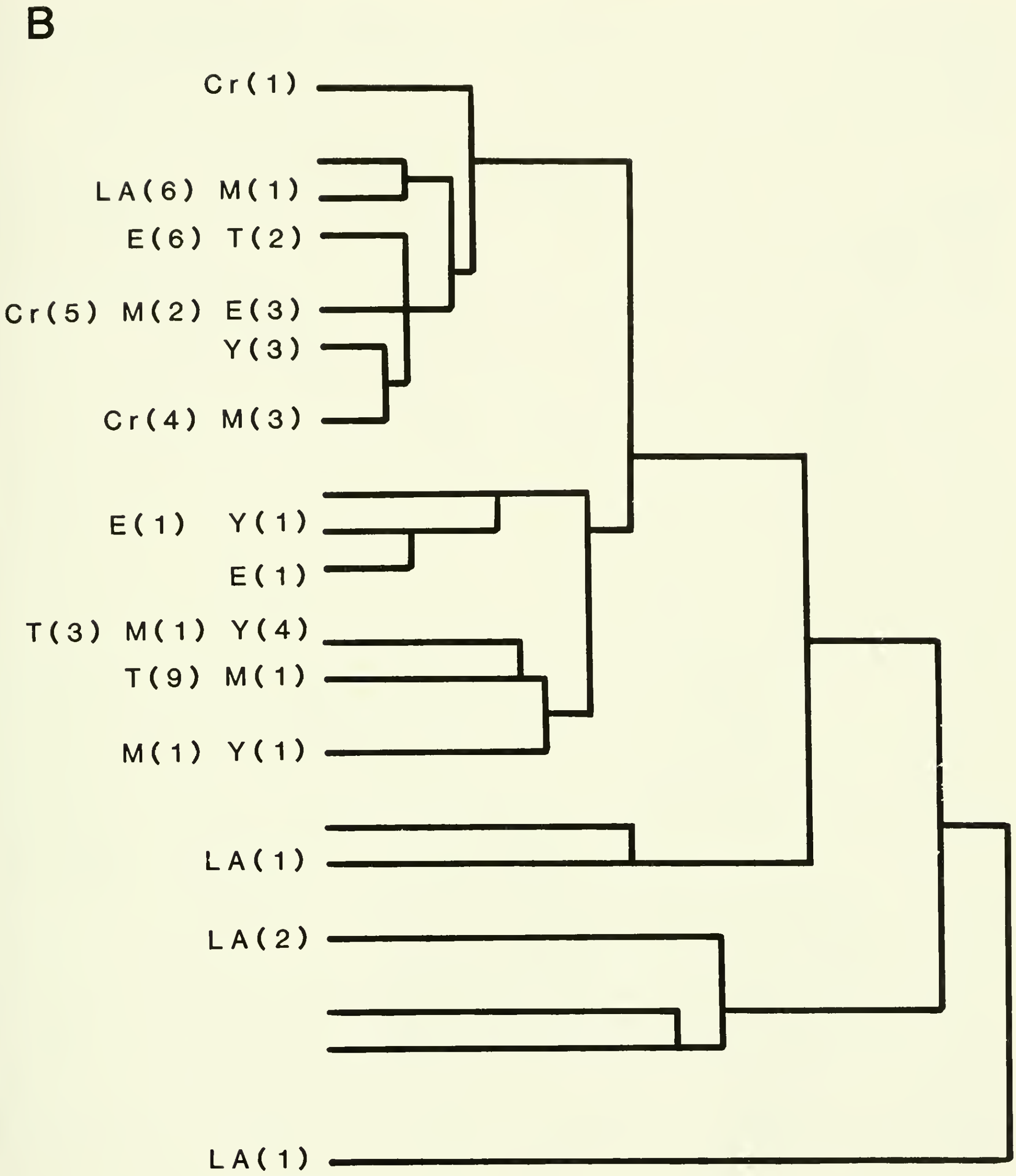
DISTRIBUTION.—*L. n. nigridia* occurs along the western slopes of the Rocky Mountains, throughout the Great Basin from southern Nevada and Utah to southern British Columbia. It is the common form along the eastern slopes of the Cascade Mountains and northern Sierra Nevada and occurs west of these ranges through xeric, low-elevation passes and river basins in California. *L. n. nigridia* also occurs throughout the coastal chaparral of southern California and into Baja California Norte. This subspecies inhabits the sagebrush-steppe habitat of the Great Basin, xeric mountain slopes, and dry lowlands. Its range appears to interdigitate with and superimpose on the ranges of the other two subspecies in some areas. However, the subspecies appear to be segregated by habitat in areas of sympatry, with *n. nigridia* inhabiting xeric shrub steppe or chaparral habitats and the other subspecies occurring in more mesic conditions, usually at higher elevations.

Lopidea nigridia aculeata Van Duzee, new status

Lopidea aculeata Van Duzee, 1917:271 (n. sp.). Carvalho, 1958:83 (cat.). Knight, 1965:11 (color, dist.). Henry and Wheeler, 1988:417 (cat.).



Figs. 8A–B. Results of UPGMA cluster analysis of color and paramere characters of 12 populations of *L. nigridia*. Letters represent populations; numbers represent the number of individuals from that population placed in that cluster. Both dendrograms are identical; to facilitate viewing and discussion, half the samples are shown on dendrogram A and the other half on dendrogram B. A, R = Mt. Rainier, WA (*L. n. nigridia*); A = Mt. Adams, WA (*L. n. nigridia*); Ca = Carbon Co., WY (*L. n. serica*); N = Elko Co., NV (*L. n. nigridia*); B = Baja California Norte (*L. n. aculeata*); J = Jackson Co., OR (*L. n. aculeata*). B, Cr = Crook Co., OR (*L. n. aculeata*); LA = Los Angeles Co., CA (*L. n. nigridia*); M = Mono Co., CA (*L. n. nigridia*); E = Elbert Co., CO (*L. n. serica*); T = Trinity Co., CA (*L. n. aculeata*); Y = Yosemite Park, CA (*L. n. aculeata*). A scale of distance values is not included because this analysis was not performed to measure morphological differences among OTUs but to illustrate groupings of OTUs using conventional taxonomic characters (see text).



Lopidea discreta Van Duzee, 1921:127 (n. sp.). Carvalho, 1958:84 (cat.). Henry and Wheeler, 1988:419 (cat.). *New synonymy*

Lopidea nigridea hirta Van Duzee, 1921:128 (n. subsp.). Carvalho, 1958:87 (cat.). Henry and Wheeler, 1988:423 (cat.). *New synonomy*

Lopidea fallax Knight, 1923:69 (n. sp.). Van Duzee, 1933:96 (note). Carvalho, 1958:84 (cat.). Henry and Wheeler, 1988:420 (cat.). *New synonymy*

Lopidea yakima Knight, 1923:69–70 (n. sp.). Carvalho, 1958:88 (cat.). Henry and Wheeler, 1988:425 (cat.). *New synonymy*

Lopidea usingeri Van Duzee, 1933:96 (n. sp.). Carvalho, 1958:88 (cat.). Henry and Wheeler, 1988:425 (cat.). *New synonymy*

Lopidea audeni Knight, 1965:9–10 (n. sp.) Henry and Wheeler, 1988:417 (cat.). *New synonymy*

Lopidea eriogoni Knight, 1965:10 (n. sp.). Henry and Wheeler, 1988:420 (cat.). *New synonymy*

Lopidea calcaria Knight, 1965:11–12 (n. sp., note). Henry and Wheeler, 1988:418 (cat.). *New synonymy*

Lopidea chamberlini Knight, 1965:12–13 (n. sp., note). Henry and Wheeler, 1988:418 (cat.). *New synonymy*

Lopidea angustata Knight, 1965:12 (n. sp.). Henry and

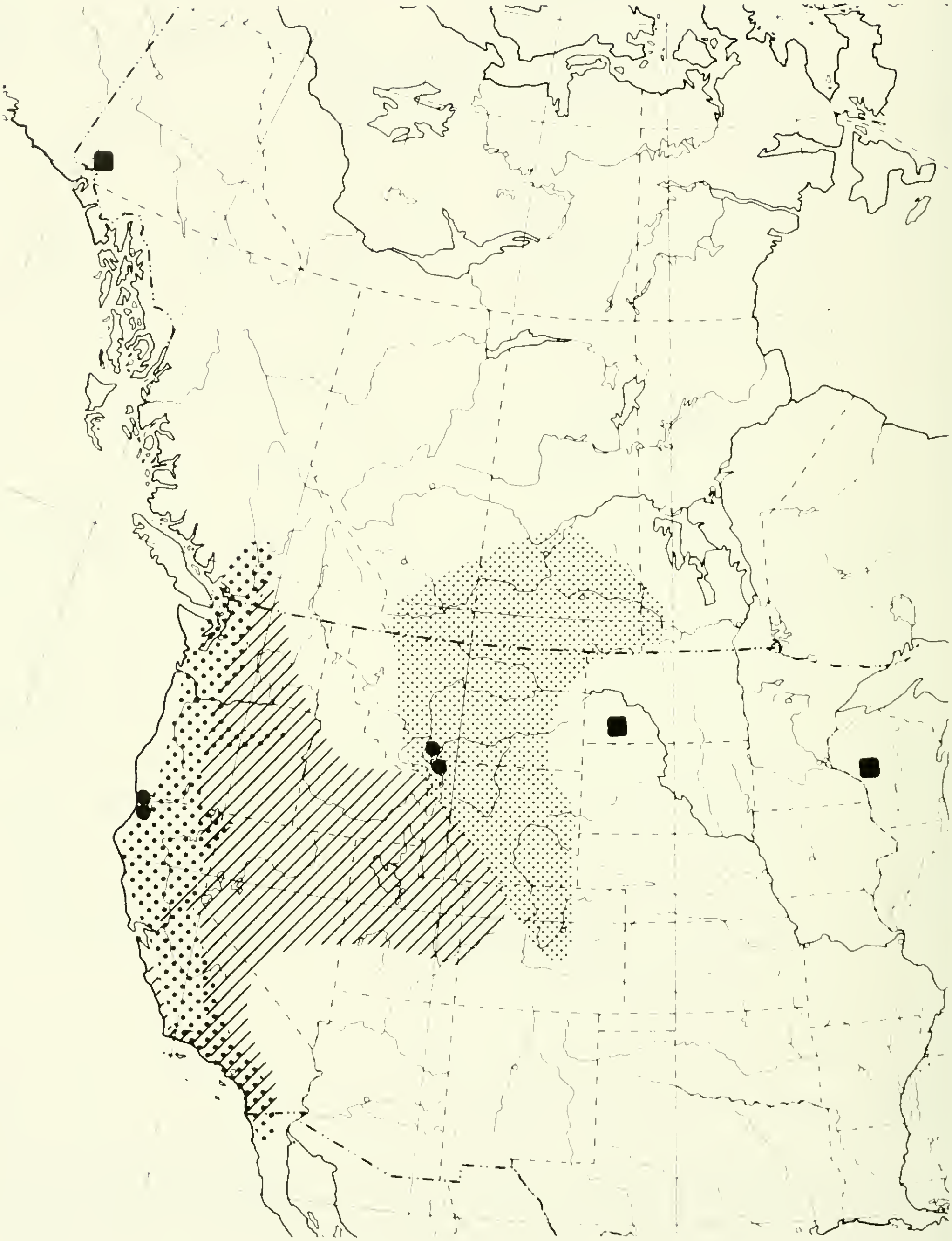


Fig. 9. Generalized distribution of *L. nigridia* Uhler. Small dots = *L. n. serica* Knight; large dots = *L. n. aculeata* Van Duzee; diagonal lines = *L. n. nigridia* Uhler; dark circles = additional localities for *L. n. nigridia*; dark squares = additional localities for *L. n. serica*.

Wheeler, 1988:417 (cat.). *New synonymy*
Lopidea rubrofusca Knight, 1965:13 (n. sp.). Henry and Wheeler, 1988:424 (cat.). *New synonymy*
Lopidea flavicostata Knight and Schaffner, 1968:75 (n. sp.). Henry and Wheeler, 1988:420 (cat.). *New synonymy*

DIAGNOSIS.—*L. n. aculeata* Van Duzee is highly variable in size and coloration (Fig. 3B). It is usually larger than *n. nigridia* and often larger than *n. serica*, but it is always more linear than the latter. In the mountains of British Columbia, Washington, and Oregon it is solid red in dorsal coloration, with more yellowish individuals found at lower elevations. Northern California individuals show some white along the embolium and cuneus, this pattern increasing in distinctness and frequency in southern populations.

This subspecies is itself highly variable, and several distinct color forms can be distinguished as follows: (1) The type specimens of *aculeata* from Seattle, Washington, are yellowish with a dark head and a large hook at the posterior angle of the apex of the right paramere. The type material is representative of populations found at low elevations in the Willamette-Puget Lowland area of Washington and Oregon. (2) *L. n. hirta* Van Duzee was described from San Miguel Island off the coast of southern California. These specimens are solid red, small, and distinctly arcuate laterally. I have seen four males from San Miguel Island in the USNM. These specimens are larger and slightly less arcuate than the type specimens of *n. hirta*, but are still different from mainland populations at that latitude. (3) Specimens from the mainland of southern California are large and linear; most have a noticeably pale embolium and cuneus. Some populations from the southern Sierra Nevada, the San Gabriel and Santa Rosa mountains of southern California, are very distinct. The hemelytra are darker, almost fuscous, the disc of the pronotum is deep red and always shiny, and the setae, especially on the pronotum, are shorter and more decumbent. The type specimens of *discreta* Van Duzee are of this form.

DISTRIBUTION.—*L. n. aculeata* occurs in the Cascade Mountains of British Columbia, Washington, and Oregon, the eastern slopes of the coastal mountain ranges in these areas, and in the Blue and Wallawa mountains of Oregon and Washington. It occurs throughout the Coastal and Sierra Nevada ranges of California. In southern California, however, the ranges of *n. aculeata* and *n. nigridia* overlap, and specimens intermediate and distinct in color pattern occur. Detailed studies of the local distributions of the color forms in this area are needed to clarify the problem.

Lopidea nigridia serica Knight, new status

Lopidea serica Knight, 1923:69 (n. sp.). Kelton, 1980:235 (dist., hosts, fig., key). Akingbohungbe, 1972:842 (note). Henry and Wheeler, 1988:424 (cat.).
Lopidea medleri Akingbohungbe, 1972:840–842 (n. sp.). Henry and Wheeler, 1988:422 (cat.). *New synonymy*

DIAGNOSIS.—*L. n. serica* Knight is larger, more robust, with the lateral margins usually arcuate and solid red in dorsal coloration, except for black on the calli and light infuscation on the clavus (Fig. 3C). Females are usually submacropterous, with the membrane of the hemelytra reduced and barely reaching the end of the abdomen. Although this is the most morphologically distinct of the subspecies, it did not appear as such in the PCA because I did not use characters such as total length and maximum width of hemelytra.

DISTRIBUTION.—*L. n. serica* occurs along the eastern slopes of the Rocky Mountains from Alberta to Colorado and east across the northern Great Plains to southern Manitoba. It appears to inhabit the mesic grasslands of the eastern Rocky Mountains and short-grass prairie systems.

There are two interesting disjunct localities for *n. serica* in western Wisconsin and southwestern Yukon Territory and adjacent Alaska (Fig. 9). Although *n. serica* might be expected to occur in the relictual prairies of Wisconsin, the Wisconsin record comes from an area of scrub oak savannah. The Yukon records are from an area along the western edge of the Yukon Plateau and at the southern edge of the Alaska-Yukon glacial refugium. This record may represent a relictual population from the refugium or the tip of the post-Pleistocene northern migration along the Interior Plateau of British Columbia, although there are no other localities north of southern British Columbia. The host plants *Lupinus* and *Astragalus* are common to both the disjunct localities.

DISCUSSION OF SPECIES

Lopidea nigridia is the original spelling used in the description by Uhler (1895). This clearly was not a *lapsus*, as I have seen Uhler determination labels using this spelling. The next citation to the species is Van Duzee (1914), who used the incorrect spelling of *nigridea*. All subsequent citations have also used the incorrect spelling.

There is confusion concerning the true identity of the species that Uhler referred to as *nigridia*. In his description (Uhler 1895), he described the color as brownish black with the outer border of the corium and cuneus rufofulvous or rufous, with no mention of white on the embolium or cuneus. However, this is clearly a contrasting dark-light pattern like that of the fuscous-white color form (*n. nigridia*). In addition, Uhler describes the anterior border of the pronotum as white, a pattern that occurs only in the fuscous-white form (*n. nigridia*) and not the red form (*n. serica*).

I located a fuscous-white specimen in the USNM bearing the label Colo. 1387. This number, 1387, corresponds with the following information in the C. F. Baker catalog: Steamboat Springs, Colo., July, C. F. Baker, ex. *Delphinium occidentale* (I attached a label with those data on the specimen). This information matches that given by Uhler for one of the specimens he examined for his original description. Knight (1923) illustrated the right paramere of another specimen from the type locality, and it is this concept of *nigridia* that has been used by all subsequent authors. Therefore, I have selected the former specimen as the lectotype of *Lopidea nigridia* Uhler and indicated such by attaching a label.

I have also seen specimens of *nigridia* with Uhler determination labels bearing the name *Lopidea obscura* Uhler, a Uhler manuscript name. It is possible that this is the name Uhler used for *L. n. nigridia*, and his description of *nigridia* referred to some other species with a contrasting light-dark color pattern. In addition, I have seen different specimens from the same locality identified by Uhler as both *nigridia* and *obscura*. It is likely, however, that the specimen I have selected as the lectotype was examined by Uhler in his description of *nigridia*.

DISCUSSION OF SUBSPECIES

Lopidea nigridia aculeata is highly variable and remains confusing to taxonomists. When discussing *aculeata*, Knight (1965) noted that specimens collected from different areas in Oregon had identical parameres but varied from yellow fuscous to red fuscous and concluded that this species was variable in color. Van Duzee (1921), when describing *discreta*, commented, "It might be best to consider this a race or variety of *nigridea*." In his discussion of *usingeri* (Van Duzee 1933), he stated, "This species, like *obscura* exhibits considerable variation in the depth of coloration."

Knight distinguished *serica* from *nigridia* by the presence of golden sericeous pubescence in *serica*, but all specimens of *nigridia* (all North American *Lopidea*, in fact) have this pubescence if it is not rubbed off.

I have seen specimens that are topotypes of *rolfsi* Knight and *rainieri* Knight that Knight originally determined as *nigridia* Uhler and other fuscous and white specimens from Idaho determined as *nigridia* Uhler. Several specimens of intermediate color pattern from California have also been determined as *nigridia* by Van Duzee.

Lopidea rubrofusca Knight was described from a single male from Monticello, Utah, and is somewhat enigmatic. It is almost solid red, typical of *n. serica*. In size and development of the hemelytral membrane, however, it is more similar to *n. nigridia;* thus, I have synonymized it with *n. nigridia*.

Analysis of the ecology, behavior, habitat, and host preference in areas of sympatry may prove that the subspecies of *L. nigridia* are actually distinct species, but morphologically they do not display differences as great as those seen between other species of *Lopidea*. In addition, more detailed studies of the populations in some areas may suggest that some of the color forms within the subspecies deserve taxonomic recognition. With the available information, however, it is more prudent to recognize the structural similarity between these populations and the rest of *nigridia* and detail the geographic variation, rather than assign names to populations with distinct color patterns.

GENITALIA

I have weighted genitalic characters heavily in forming a species concept for *L. nigridia*. This is based on examinations of these structures throughout the genus and in related

Orthotylini. My analyses of paramere structure show no geographic pattern or distinction among subspecies. It is possible that incipient speciation has occurred in this complex and that it is not reflected in paramere morphology. This is most plausible for *L. n. nigridia* and *L. n. serica* in the northern and eastern parts of the range, where they retain distinct color patterns and exhibit the greatest differences in the shape of the dorsal spicula. Other species of Miridae also display geographic variation in size, vestiture, or color, including *Irbisia brachycera* (Uhler) (Schwartz 1984) and *Pilophorus tibialis* Van Duzee (Schuh and Schwartz 1988).

Although the parameres and vesicae have been used as taxonomic characters in the Miridae for at least 40 years, few studies have described the within-species variation of these structures. Stonedahl and Schwartz (1986) illustrate the variation in paramere structure for some species of *Pseudopsallus*. Stonedahl (1988) described clinal variation in the size and shape of the vesica of *Phytocoris yollabollae* Bliven and recognized two biotypes of *P. fraterculus* Van Duzee based on geographic differences in male genital structures. He found that other species of *Phytocoris* such as *P. tenuis* Van Duzee are highly variable in size, color, and genital structure; yet none of these variables were correlated with each other, nor did any show clear patterns of geographic variation. Detailed documentaion of variation in genitalic structures is rare for any group of Heteroptera. Several examples are available for the auchenorrhynchous Homoptera, however. *Euscelis incisus* (Kirschbaum) exhibits seasonal variation (Muller 1954), and *E. incisus* Brulle shows temperature-induced variation (Muller 1957) of the aedeagus. Wagner (1955) illustrated extreme clinal geographic variation in the aedeagus of *Philaenus spumarius* (L.). Other studies have documented the intra- and interpopulational variation of aedeagal characters in this group (Wagner 1967, Le Quesne and Woodroffe 1976, Oman 1987). Studies of the infraspecific variation in spicula shape in the orthotyline Miridae are greatly needed. In *L. nigridia* the dorsal spicula varies from straight and blunt to curved and pointed (Fig. 7). The ventral spicula can also be twisted and varied in its curvature and dentation.

COLOR

The distinction between the subspecies in some areas and their discrete distributions probably reflects some degree of genetic segregation. This pattern might be interpreted as a species-level phenomenon; however, the subspecies are almost identical morphologically and do not appear to be segregated by host plant, as are other species of *Lopidea*. *L. n. aculeata*, however, shows inter- and intrapopulational variation in color pattern from fuscous-red or solid red to red-white.

Although I have placed subspecies determination labels on all specimens I examined for this study, the assignment of some populations to *L. n. nigridia* or *n. aculeata* is equivocal. For example, I have examined two series of specimens both collected from Mokelumne Hill, Calaveras Co., California, but from different years. One series exhibits the fuscous-white color pattern typical of *n. nigridia*, while the other series is a lighter red-white color typical of *n. aculeata*. There are a few additional localities from which two of the subspecies have been collected, although not from the same year or dates. Because of the lack of detailed local geographic variation, habitat preferences, and biological data from these areas, I refrain from making suggestions regarding hybrid suture zones and intergradation for these forms of *L. nigridia*. This suggests the possibility that these forms are not distinct lineages but only ecotypes.

Because temperature is known to affect the deposition of red and black pigments in Heteroptera (Knight 1924, Aldrich 1986), some of the color variation of *L. nigridia* is undoubtedly environmentally induced, and different color forms could develop at the same locality at different times of the year or different years. I have reared two of the subspecies, *n. nigridia* and *n. aculeata*, under three temperature regimes, 13 C, 21 C, and 33 C. Individuals of both subspecies reared at 13 C were clearly darker than those reared at 33 C; those reared at 13 C exhibited fuscous or black coloration on areas of the head, pronotum, and hemelytra that were red in the specimens reared at 33 C. However, the pale embolium and cuneus of the *n. nigridia* individuals were not affected by temperature, nor was the red color of these structures affected in the specimens of *n. aculeata*.

The pattern of color variation seen in *L. nigridia* is common in the genus *Lopidea*. Several other western species, such as *marginata* Uhler, *taurina* Van Duzee, and *chelifer* Knight, also have populations of solid red individuals and other populations with white margins of the hemelytra. The same distribution pattern of the *nigridia* subspecies is seen in other species with color polymorphism; the red-white or black-white forms occur in the Intermountain region, and the solid red forms occur further north and in the Rocky Mountains. It is also interesting that the distribution of the subspecies of *nigridia* corresponds to the distribution of other species of *Lopidea* of constant color. Species with contrasting red-white or fuscous-white patterns tend to predominate in the Intermountain region where the fuscous-white *n. nigridia* is found, and solid red or red-fuscous species are more common in the northern U.S. and Canada and the Great Plains where only the red *n. serica* occurs.

Other explanations such as host plant–induced color patterns (Palmer and Knight 1924a, 1924b) or selection for a certain pattern by different predator complexes (McIver and Lattin, in press) are equally viable.

BIOLOGY

The population biology of *Lopidea nigridia* Uhler in eastern Oregon was described in detail by McIver and Asquith (1989). At their study site, *nigridia* has one generation per year and overwinters in the egg stage in the tissue of its host plant, *Lupinus caudatus* Kell. Nymphs appear from late April to early June, most individuals achieving adulthood by mid-June. Oviposition is from late June through July, and most activity ends by early August.

In California, adults have been collected from 4 April to 1 September but are most commonly taken between 15 May and 15 July, with the average collection date being the third week in June. In other parts of the range adults emerge later in the season and are most common between 7 June and 15 August, with an average collection date in the second week of July.

Lopidea nigridia has been collected from at least 28 different genera of plants. West of the Rocky Mountains more than 48% of the host plant records are *Lupinus*. Testing this observation against a null hypothesis of an equal number of collections from all recorded hosts shows that *nigridia* is collected from *Lupinus* more often than would be expected by chance ($X^2 = 326.26$, $p < .001$, $N = 75$, DF $= 25$). In addition, four of five confirmed breeding records were on *Lupinus* and one on *Astragalus*.

In the Great Plains greater than 50% of the records are of *Astragalus*. This switch in host preference corresponds with the distribution of the subspecies *L. n. nigridia* and *n. serica*. Another mirid, *Coquillettia insignis* Uhler, which is typically associated with *Lupinus* in western North America, also feeds on *Astragalus* in Colorado and Wyoming (McIver and Stonedahl 1987). This pattern may reflect a change in the abundance and availability of the two host plants.

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POLLINATION EXPERIMENTS IN THE *MIMULUS CARDINALIS–M. LEWISII* COMPLEX

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ABSTRACT.—Experimental sets of *Mimulus cardinalis* and *M. lewisii* plants were (1) exposed to pollinators and (2) shielded from pollinators at study sites in Red Butte Canyon and Big Cottonwood Canyon, Wasatch Mountains, Utah. The exposed plants produced 1,535 seedlings and the shielded plants only 1. Clearly, seed production is dependent upon cross-pollination. A few syrphid flies were observed visiting the flowers but no hummingbirds or bumble bees, although the latter two have been reported as the main pollinators of *M. cardinalis* and *M. lewisii*, respectively. No interspecific hybrids were produced even through the species are fully interfertile, indicating that pollinators are faithful to their species or that different parts of their bodies pick up and carry pollen to the two different species.

Theoretically, changes in flower color or morphology may lead to a change in pollinators. How great must these changes be to affect reproductive isolation and launch the different populations on divergent evolutionary paths? Before exploring this question, it is necessary to establish whether or not reliance upon different pollinators is effective in reproductively isolating sympatric populations.

The *Mimulus cardinalis–M. lewisii* complex of interfertile species and varieties appears to be an excellent group to use in investigating this latter question (Vickery 1978). The species and their various populations differ greatly in the degree of interfertility (Vickery 1978, Vickery and Wullstein 1987); however, the two populations used in this study are fully interfertile and produce numerous F_1 and F_2 hybrids when artificially pollinated (unpublished data). The F_1 hybrids are pink flowered, and the F_2 hybrid populations segregate 3:1, various tints of pink to various shades of red (Vickery and Olson 1956, and unpublished data).

Mimulus cardinalis has flower color morphs of red, red-orange, and yellow. Its corolla lobes are sharply reflexed along the corolla tube, the corolla tube being 5 mm or less in diameter and 30–33 mm long. The bilabiate, sensitive stigma is exserted 16–20 mm. The two pairs of anthers, exserted 12–15 mm, are closely appressed to the style, one below the other and immediately below the stigma. When a hummingbird probes the flower for nectar, its forehead brushes the stigma and anthers, picking up pollen grains that may be deposited on the stigma of the next flower. *Mimulus cardinalis* is such a typical hummingbird flower that it was used as the cover illustration of Grant and Grant's (1968) book, Hummingbirds and Their Flowers.

Mimulus lewisii has flower color morphs of light lavender and deep magenta. Its corolla lobes are thrust forward in the light lavender–flowered race and are gently recurved in the deep magenta–flowered race. The corolla throat is open and approximately 10 mm wide by 7 mm high in the lavender-flowered race of the Sierra Nevada and approximately 12–15 mm wide and high in the magenta-flowered race of the Rocky Mountains. The corolla tubes are approximately 25 mm deep in both races. The sensitive, bilabiate stigma is included and is about 2 mm below the corolla orifice in the Sierran race. In the Rocky Mountain race the stigma is included but on a level with the orifice. The anthers occur in pairs, one below the other and 1–2 mm below the stigma in both races. *Mimulus lewisii* flowers are well adapted for bees landing on the labellum petal of the corolla and climbing into the flower for nectar and/or pollen. Their bodies brush the stigma and anthers and pick up pollen which they then may deposit on the stigma of the next flower. *Mimulus lewisii* has textbook-typical bee flowers (Faegri and van der Pijl 1979).

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Mimulus cardinalis ranges from southern Oregon south to central Baja California, and from the California Coast Range inland to mid-elevations in the Sierra Nevada (Vickery and Wullstein 1987). The lavender-flowered race of *M. lewisii* occurs at elevations higher than *M. cardinalis* in the Sierra Nevada. The magenta-flowered race ranges from the northern Sierra Nevada north to Alaska and east to the Rocky Mountains (Vickery and Wullstein 1987). The two species rarely overlap and then only when seeds of *M. lewisii* wash down into the range of *M. cardinalis* and become established as ephemeral populations on streamsides, principally in the central Sierra Nevada (Hiesey et al. 1971). The sympatric populations flower at the same time, which heightens the importance of their reproductive isolation by different pollinators.

Both species produce nectar throughout the day, although the nectar production of *M. cardinalis* is far more copious than that of *M. lewisii*.

Before the main, long-range question of the effect of differences in flower color and/or shape on the pollinators can be investigated, it is necessary to establish some basic facts. First, do *M. cardinalis* and *M. lewisii* require the service of pollinators? Or, do they self-pollinate, at least to some extent? Second, if pollinators are required, which ones normally visit the flowers of the two species? Once the norms are ascertained, then the effect of different colors and/or shapes can be determined. Third, are the pollinators faithful to their species? Or, does cross-pollination occur between the two species? That is, would a difference in pollinators isolate the two species reproductively? Or, only partially? Or, would the differences between the species tend to swamp out? The purpose of this study is to answer these intrinsically interesting basic questions and, in addition, to provide the necessary foundation data for the long-range study.

MATERIALS AND METHODS

Plants of typical red-flowered *M. cardinalis* Douglas (culture 13313 from Cedros Island, Baja California) were grown from seed in the University of Utah greenhouse, as were plants of magenta-flowered *M. lewisii* Pursh (culture 5875 from Alta, Utah), typical of the Rocky Mountain race. The seedlings were transplanted first into 4″ pots and then, when large enough, into deep 8″ pots. The bigger pots allowed the plants to grow larger (20–60 cm high) and produce many flowers for the field studies.

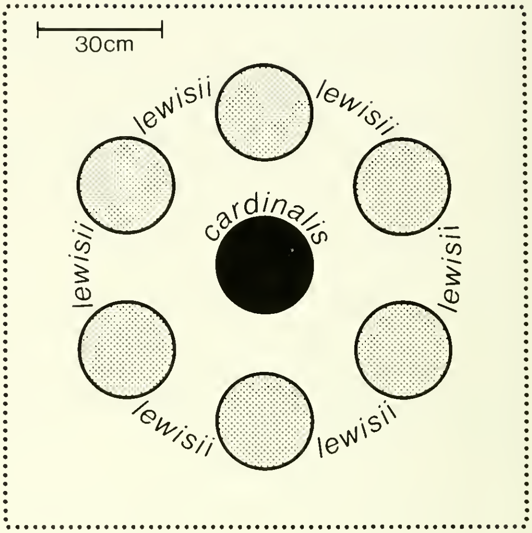

Fig. 1. Arrangement of potted plants in the experimental sets. The reciprocal arrangement was of *M. lewisii* in the center surrounded by six *M. cardinalis* plants. The dotted line indicates the location of the screen cage in the pollinator exclusion trials.

The field tests were carried out at two sites in the Wasatch Mountains of Utah. The first location was in the Red Butte Canyon Natural Area, Salt Lake County, and the second, at Silver Fork in Big Cottonwood Canyon, also Salt Lake County. In Red Butte Canyon the pots of plants were placed on the wet delta at the head of the reservoir, elevation 5,360 feet, so they could be watered naturally. At Silver Fork the pots of plants were placed in the meadow, elevation 7,800 feet, below Silver Fork Lodge, and were watered daily by Luther Light.

The plants were arranged in experimental sets of seven plants. In each set the center pot contained a plant of one species, e.g., *M. cardinalis;* and a whorl of six pots surrounding it each contained one plant of the other species, e.g., *M. lewisii* (Fig. 1). This arrangement was designed to facilitate cross-pollination, should it occur.

At the Red Butte Canyon site, four experimental sets were exposed to the pollinators. Two sets had *M. cardinalis* as the center plant surrounded by *M. lewisii* plants, and two sets had *M. lewisii* in the center surrounded by *M. cardinalis*. In addition, four corresponding sets were placed in 1 × 1 × 1-m screen cages (plastic mesh, 20 threads per inch, pore size 1 × 1 mm) designed to exclude pollinators. The same experimental design was repeated at the Big Cottonwood Canyon study site. The first study site was in a streamside, partially shaded, maple–box elder forest; the second was in an open meadow in the aspen-spruce forest. Two contrasting sites were employed as controls in case different pollinators occurred in different habitats and at different elevations in the canyons.

At the beginning of the experiments all capsules and flowers were removed. New flowers began opening the next day. The plants were observed to note pollinator visits for a total of 20 hours for each experimental set. The observations were one-hour periods scattered from dawn to dusk on different days. Experiments were run for one month, by which time new flowers had opened on most plants; they had been exposed to pollinators (that is, the uncaged sets); and capsules had formed and were starting to ripen. Plants were then returned to the greenhouse, and capsules on plants of both exposed and shielded sets were harvested as they ripened. Seeds set were not counted inasmuch as the number of seedlings produced seemed a more meaningful measure of pollinator success or selfing rate.

In the summer of 1984 all seeds produced by the peripheral whorl of plants in each experimental set were sown together in one pot, and seeds produced by the plant in the central pot were sown in another. Resulting seedlings were scored as to whether they were of parental type, indicative of pollinator faithfulness, or hybrids, indicative of pollinator promiscuousness, that is, pollinators visiting both species. The F_1 hybrids, which have leaves intermediate in width between the broad leaves of *M. cardinalis* (13013) and the narrow leaves of *M. lewisii* (5875), can be distinguished at an early stage. Nevertheless, the seedlings were grown until they flowered and exhibited either the unambiguous F_1 pink color or the parental red (*M. cardinalis*) or magenta (*M. lewisii*).

RESULTS AND DISCUSSION

Are pollinators necessary? Results of this research indicate a resounding yes! All plants in cages set a total of only one seed that germinated and grew into a seedling (Table 1). It was a vigorous *M. cardinalis* plant from the central plant in one of the Red Butte Canyon sets. In contrast, plants in the sets exposed to pollinators produced a total of 1,535 seeds that germinated and grew into seedlings. Of these, 1,047 were *M. cardinalis* and 488 were *M. lewisii*. While there were equal numbers of plants, there were more *M. cardinalis* flowers. Hybridizations were possible in three of the eight experimental sets. The results are very clear despite the heavy depredations by deer and the lack of flowering in the other sets (Table 1).

Pollinator observations revealed the presence of Broad-tailed Hummingbirds and bumble bees at both sites and syrphid flies at the Red Butte Canyon site. Hummingbirds and bumble bees flew near the *Mimulus* plants at both sites but, surprisingly, were not observed visiting the flowers. However, in the Red Butte Canyon experiments, small syrphid flies visited both species occasionally, but not on the same foraging bout (1–5 minutes, 1–3 flowers) nor often enough to account for the observed seed sets. There were only five total visits (at scattered times), and the only pattern revealed was that syrphids visited the lower-elevation experiments of Red Butte Canyon but not the higher-elevation experiments of Big Cottonwood Canyon. The flies appeared to be foraging for pollen inasmuch as they walked all over the flowers, including the anthers and pistils.

Of the 1,535 seedlings produced, not one was a hybrid. This was true also in the progeny grown from plants of a natural, sympatric population of both species in the Yosemite Valley by Hiesey et al. (1971). Apparently the pollinators are effectively faithful to each species both in the Wasatch Mountains and the Sierra Nevada.

The study raises some intriguing questions. Why were hummingbirds and bees not observed pollinating the flowers when the Carnegie study (Hiesey et al. 1971) showed

Table 1. Seedlings produced from the seeds set by *M. cardinalis* and *M. lewisii* plants in Red Butte Canyon and Big Cottonwood Canyon (1) when exposed to pollinators and (2) when shielded from pollinators by cages. Plants were arranged in sets consisting of a center plant of one species surrounded by a whorl of six plants of the other species (see Fig. 1).

		Number of seedlings resulting	
Set number	Composition of set	Exposure to pollinators	Shielded from pollinators
Red Butte Canyon experiments			
#1	1 central *cardinalis*	0*	1 *cardinalis*
	6 peripheral *lewisii*	0*	0
#2	1 central *cardinalis*	0*	0
	6 peripheral *lewisii*	71 *lewisii*	0
#3	1 central *lewisii*	190 *lewisii*	0**
	6 peripheral *cardinalis*	350 *cardinalis*	0**
#4	1 central *lewisii*	0**	0
	6 peripheral *cardinalis*	420 *cardinalis*	0
	Total *cardinalis* seedlings	770	1
	Total *lewisii* seedlings	261	0
	Total F_1 hybrid seedlings	0	0
Big Cottonwood Canyon experiments			
#5	1 central *cardinalis*	184 *cardinalis*	0
	6 peripheral *lewisii*	137 *lewisii*	0**
#6	1 central *cardinalis*	93 *cardinalis*	0
	6 peripheral *lewisii*	90 *lewisii*	0**
#7	1 central *lewisii*	0*	0
	6 peripheral *cardinalis*	0*	0
#8	1 central *lewisii*	0*	0
	6 peripheral *cardinalis*	0*	0
	Total *cardinalis* seedlings	277	0
	Total *lewisii* seedlings	227	0
	Total F_1 hybrid seedlings	0	0
Grand total *cardinalis* seedlings		1,047	1
Grand total *lewisii* seedlings		488	0
Grand total F_1 hybrid seedlings		0	0

*Capsules on experimental plants eaten by deer.

**Failed to flower during experiment

them to be the main pollinators of *M. cardinalis* and *M. lewisii*? What would their visits show about temporal partitioning? Or, perhaps, morphological partitioning for pollen transfer on different parts of the pollinator's body? Are there significant differences in quantity and sugar content of the nectar produced by the flowers that might affect pollinator preferences and visits?

In conclusion, despite the questions raised for future studies, these experiments demonstrated that neither *M. cardinalis* nor *M. lewisii* self-pollinates under natural conditions; at least, the rate is less than .1%. Clearly, pollinators are required for seed set. Only syrphid flies were observed actually pollinating the flowers, although hummingbirds and bumble bees are probable pollinators also (Hiesey et al. 1971). The experiments showed that the pollinators (seen and unseen) are effectively faithful to their own *Mimulus* species. So, (1) pollinators are required, (2) the only observed pollinators are the small syrphid flies, and (3) the pollinators are effectively faithful to their species, either on each foraging bout or by using species-specific parts of their bodies for pollen transfer.

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OBSERVATIONS ON THE DWARF SHREW (*SOREX NANUS*) IN NORTHERN ARIZONA

Howard J. Berna[1]

ABSTRACT.—Observations of 23 dwarf shrews (*Sorex nanus*) at Fracas Lake in Arizona extend the range of this uncommon shrew northward on the Kaibab Plateau and provide further information regarding the ecology and habitat requirements of this species. Shrews were captured in a previously unreported habitat type (Rocky Mountain montane conifer forest; Brown 1982). This study illustrates the usefulness of intensive, long-term studies and faunal surveys using pitfall traps.

Since Merriam discovered the dwarf shrew in 1895, it has been considered a rare species. For 70 years after it was named, *Sorex nanus* was known from only 18 specimens (Hoffmann and Owen 1980). With the recent use of pitfall traps this number has increased greatly (e.g., 81 *S. nanus* in Colorado [Armstrong et al. 1973], 48 in Wyoming [Brown 1967], and 16 in Arizona [Marshall and Weisenberger 1971]).

The dwarf shrew is one of many mammal species inhabiting an archipelago of forested montane islands in the western United States (Lomolino et al. 1989). The species is currently known from Montana, Wyoming, South Dakota, Colorado, Utah, New Mexico, and Arizona (Hoffmann and Owen 1980). *Sorex nanus* is known from reports of only 20 specimens from three areas in Arizona (Fig. 1; Hoffmeister 1986); no new Arizona localities have been reported for 15 years.

The first *Sorex nanus* in Arizona was collected on 17 September 1937 from the Kaibab Plateau, Coconino Co., 14.5 km east of Swamp Point within the Grand Canyon National Park (GCNP, North Rim) at an elevation of about 2,439 m (Schellbach 1948). On 28 August 1973 another specimen was taken 5.6 km from the first record, near Kanabownits Springs within the GCNP (Ruffner and Carothers 1975). Both areas typically contain mixed-conifer forest, *Picea pungens*, *Picea engelmannii*, *Abies lasiocarpa*, *Abies concolor*, *Pseudotsuga menziesii*, and *Populus tremuloides* (subalpine conifer forest; Brown 1982). Another specimen of the dwarf shrew was reported from the Kaibab Plateau by Hoffmeister (1955). It was found in the Kaibab Lodge, VT Ranch, when the lodge was opened in April 1944. The lodge is surrounded by extensive grassy meadows to the east and subalpine conifer forest to the west.

A single specimen was collected on 14 August 1959 in the White Mountains of Greenlee Co., near Hannagan Meadows, in spruce-fir forest habitat (subalpine conifer forest; Brown 1982), at an elevation of 2,805 m, extending the range into the second area of the state (Bradshaw 1961). To my knowledge, there have been no recent records of *Sorex nanus* from this area.

Marshall and Weisenberger (1971) trapped *Sorex nanus* in Arizona in a third area, near Flagstaff, in the Inner Basin of the San Francisco Mountains at elevations between 2,865 and 3,293 m. During the summer of 1969 eight specimens were taken in rocky talus and eight from mesic subalpine meadows and surrounding spruce-fir forest. The specimens reported in this article extend the known range of *Sorex nanus* in Arizona northward on the Kaibab Plateau and describe a new habitat for this species in Arizona.

STUDY AREA

The study area was Fracas Lake, Coconino Co., 9.6 km south-southwest of Jacob Lake (36°37′52″N, 112°14′20″W, elev. 2,514 m). Fracas Lake is a permanent, natural limestone

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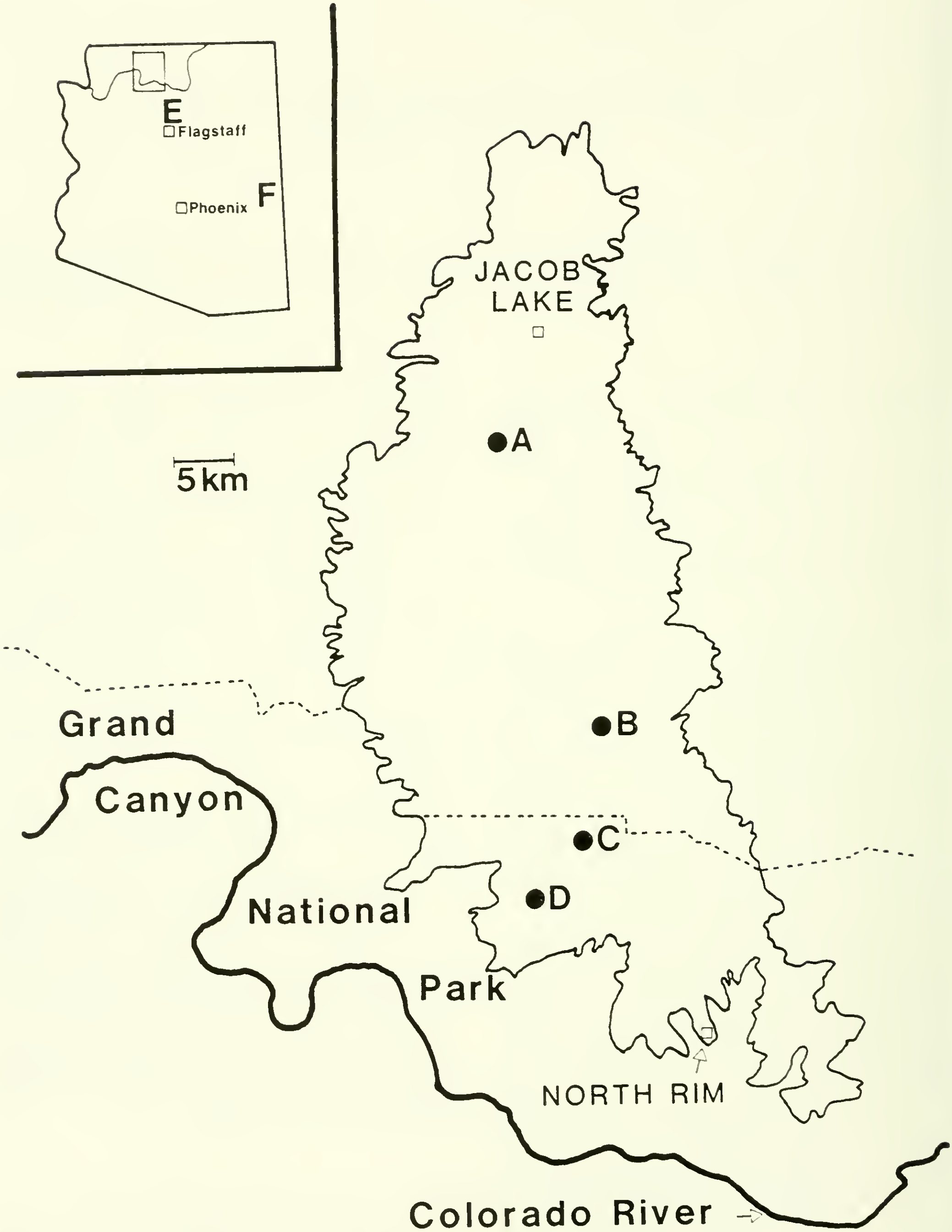
E
Flagstaff
F
Phoenix
JACOB LAKE
A
5 km
B
Grand Canyon National Park
C
D
NORTH RIM
Colorado River

Fig. 1. Collection sites of *Sorex nanus* in Arizona. Boxed area of state enlarged. Contour line outlines Kaibab Plateau at elevation 2,195 m; A, this study; B, Hoffmeister 1955, C, Schellbach 1948, D, Ruffner and Carothers 1975; E, San Francisco Peaks (Marshall and Weisenberger 1971); F, Hannagan Meadows (Bradshaw 1961).

sinkhole basin less than 1 ha in area, varying in depth from 0.5 to 1.5 m.

The terrestrial habitat surrounding Fracas Lake is dominated by ponderosa pine (*Pinus ponderosa*) and a few aspen (*Populus tremuloides*) about 15–25 m from the edge of the lake (Rocky Mountain montane conifer forest; Brown 1982). There are a few small patches of mixed-conifer forest within 1 km of the lake; however, *Pinus ponderosa* is the dominant conifer for several square kilometers around the lake. At ground level there is little vegetation in the understory. Common shrub species include *Juniperus communis*, *Ceanothus fendleri*, *Rosa fendleri*, and *Ribes inebrians*. Short grasses occur in the open area around the lake. Only a few fallen trees and woody debris piles exist near the lake.

Mammal species (excluding bats) that I have collected or observed in association with *Sorex nanus* at this locality include: *Spermophilus lateralis*, *Eutamias umbrinus*, *Eutamias minimus*, *Tamiasciurus hudsonicus*, *Sciurus aberti kaibabensis*, *Thomomys talpoides*, *Peromyscus maniculatus*, *Microtus longicaudus*, *Erethizon dorsatum*, *Odocoileus hemionus*, and an occasional *Sylvilagus nuttalli*, *Canis latrans*, *Mustela frenata*, and *Mustela erminea* (Berna 1990).

METHODS

Sorex nanus was captured at Fracas Lake during a two-year study of the Arizona tiger salamander (*Ambystoma tigrinum nebulosum*). Fracas Lake was completely surrounded by an aluminum drift fence 214.6 m in circumference. The 40-cm-high fence was buried 7–10 cm below ground level. Two 4.5-gallon buckets were buried as pitfall traps at each of 27 stations, approximately 7 m apart. The pitfall traps were adjacent to the fence, with one bucket on each side of the fence per station. The average distance of the drift fence to the water was 8 m. Pitfall traps were checked daily from 17 May to 15 September 1988. They were checked every two weeks from 15 September until 19 November 1988 and then daily from 27 April 1989 until 14 September 1989. After 14 September they were checked once every week until 18 October 1989. Therefore, trapping occurred for 186 days in 1988 (10,044 trap nights) and 174 days in 1989 (9,396 trap nights).

TABLE 1. Monthly captures of *Sorex nanus* at Fracas Lake, Coconino Co., Arizona, in 1988 and 1989.

Month	1988	1989
April	—	0
May	0	0
June	1	3
July	1	3
August	6	6
September	3	0
October	0	0
November	0	—

Standard measurements of specimens were taken, and shrews were aged by tooth wear (Diersing and Hoffmeister 1977) and placed into two categories.

Minimum and maximum temperatures and precipitation were monitored daily throughout the study periods. Air temperatures varied from −9 to 42 C, and shrews were caught on evenings when minimum temperatures varied from 1 to 10 C. The total number of days with rain during the study in 1988 was 58, with a total rainfall of 249 mm. It rained during 34 study days in 1989, with a total rainfall of 130.5 mm.

RESULTS AND DISCUSSION

I collected 23 *Sorex nanus* during this study (Table 1). Specimens were positively identified as *Sorex nanus* based on small body size (less than 52 mm), upper third unicuspid smaller than fourth, and presence of medial tines on first incisor (Junge and Hoffmann 1981, Hoffmeister 1986). One specimen was kept as found in a mummified state, six were captured alive and released, seven were preserved as skins plus skulls, and nine were fixed in 10% formalin and later stored in 65% ethanol. Specimens have been deposited in the mammal collection at Arizona State University.

Standard body measurements, sex, and age of several dwarf shrews are reported in Table 2. Some shrews were partially eaten by carrion beetles in pitfall traps, making sex determination impossible. Mean body measurements (in mm, range in parentheses) were as follows ($n = 16$): total length 75 (71–77), tail length 36 (34–39), hindfoot 9 (8–10), ear from notch 6 (4–7). Mean body mass was equal to 2 g ($n = 12$). Reproductive condition was unambiguous for only one of the

TABLE 2. Standard measurements (length in mm, mass in g) of body size, sex, and age (Ad = adult, Juv = juvenile) of *Sorex nanus* captured at Fracas Lake during 1988 and 1989. TL = total length, T = tail length, HF = hindfoot length, E = length of ear from notch.

Date	Age	Sex	TL	T	HF	E	Mass
1988							
23 June	Ad	male	82	36	9	7	2.5
16 July	Ad	female	81	37	9	5	2.0
1 August	Ad	male	79	36	9	7	2.0
6 August	Juv	female	74	36	9	6	2.0
17 August[a]	—	?	—	—	—	—	—
21 August	Juv	male	73	34	7	6	2.0
23 August	Juv	male	72	38	9	6	1.8
30 August	Juv	male	78	38	10	7	2.0
2 September[b]	—	?	—	—	—	—	—
7 September	—	? (mummified specimen, no measurements)					
1989							
8 June	Ad	?	76	37	10	6	—
10 June	Ad	female	74	38	10	7	—
11 June	Ad	?	76	36	9	6	—
5 July	Juv	male	74	36	8	5	2.0
21 July	Juv	male	71	36	8	4	1.8
27 July	Juv	?	71	35	9	7	—
10 August[a]	—	?	—	—	—	—	—
12 August[b]	—	?	—	—	—	—	—
21 August	Juv	male	72	38	10	6	2.0
25 August	Juv	male	77	39	10	6	1.8
26 August	Juv	male	72	36	10	6	1.8

[a] Captured alive and released unharmed.

[b] Two live specimens caught on this date and released unharmed.

three females captured. The female captured on 16 July 1988 had three developing follicles greater than 2 mm in diameter.

All shrews were collected in pitfall traps outside the drift fence, suggesting that the shrews do not reside within the fenced area but use the area only as a foraging site. Juveniles were caught in July and August (Table 2), and this activity may correspond to the period of juvenile dispersal. All shrews were collected in the morning, although pitfall traps were checked twice daily. Shrews were more frequently caught on days with measurable rainfall (17 of 23, or 74% caught on days with rain). This may be due to increased foraging range when the stress of water requirements of the shrew is lessened, or it may simply correspond to increased prey activity.

Potential prey for *Sorex nanus* at this locality include spiders, which were abundant early in the season (April-June); tenebrionid beetles, common throughout the study period (May-September); and the following families and orders of invertebrates that appeared in pitfall traps at various times during the study: Formicidae, Carabidae, Scarabidae, Curculionidae, Coccinelidae, larval lepidopterans, orthopterans, and a few hemipteran and homopteran species.

Observations of three live shrews caught in pitfall traps suggested that dwarf shrews avoid tenebrionid beetles. In two instances the shrew and a few tenebrionid beetles were all that remained alive in the pitfall trap. Shrews seemed to favor carabid beetles, which they attacked voraciously with bites to the head and thorax followed by a quick retreat, and then repeated until the beetle was subdued and consumed. I also observed a shrew feeding on ants while it was in a pitfall trap.

Shrews are known to take a variety of small vertebrates as prey (Hoffmeister 1986). On two occasions in this study a *Sorex nanus* was found in the same pitfall trap as an adult tiger salamander (*Ambystoma tigrinum nebulosum*). The salamanders (snout-vent length 85–90 mm) were unharmed on both occasions, but in one instance the shrew was found dead. This may indicate an unwillingness to consume these large vertebrates with toxic skin secretions, or it may suggest that adult salamanders are much too large to be considered part of the ordinary diet of even the hungriest *Sorex nanus*.

These recent observations extend the known range of *Sorex nanus* northward on the Kaibab Plateau in Arizona 25 km from the previous record of Hoffmeister (1955). The habitat at this locality is dominated by *Pinus ponderosa*, which is a new habitat type recorded for this species in Arizona. In this study *Sorex nanus* was collected within 8 m of water, unlike previous records for Arizona (Hoffmeister 1986).

Future surveys using pitfall traps elsewhere on the Kaibab Plateau, and on other southwestern montane "islands," would be beneficial in determining the abundance and distribution of *Sorex nanus* in the southern portions of its range. They would also provide a clearer definition of the habitat requirements of this species.

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FUNGI ASSOCIATED WITH SOILS COLLECTED BENEATH AND BETWEEN PINYON AND JUNIPER CANOPIES IN NEW MEXICO

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ABSTRACT.—The soil fungal community beneath pinyon (*Pinus edulis* Engelm.) and one-seeded juniper (*Juniperus monosperma* [Engelm.] Sarg.) tree canopies is described and compared with fungi from adjacent interspace soils dominated by blue grama (*Bouteloua gracilis* [H.B.K.] Lag.). Significantly higher organic matter contents and fungal propagule levels were found in soils beneath pinyon and juniper trees than in interspace soils. Soils under pinyon and juniper trees contained similar chemical, physical, and biological properties and, consequently, many groups of fungi in common (64% of the species isolated were common to both). In contrast, soil fungi in adjacent interspace soils were vastly different from those collected in soils beneath pinyon and juniper canopies (44% and 48% species in common, respectively). Soil fungi that were isolated more often from pinyon-juniper soils than from interspace soils included *Absidia* spp., *Beauvaria* spp., *Gliocladium* spp., *Mucor* spp., *Penicillium cyclopium*, *P. fasciculata*, *P. frequentans*, *P. restrictum*, *Thamnidium* spp, and *Trichoderma* spp. Soil fungi that were isolated more often in interspace soils than in pinyon or juniper soils included *Aspergillus alutaceus* spp., *A. fumigatus*, some *Fusarium* spp., *Penicillium luteum*, and *P. talaromyces*.

Pinyon (*Pinus edulis* Engelm.) and one-seeded juniper (*Juniperus monosperma* [Engelm.] Sarg.) trees have been reported to accumulate significant amounts of organic matter and nutrients beneath their canopies (Barth 1980, Tiedemann 1987, Klopatek 1987). Although the soil nutrient content directly under pinyon and juniper trees is higher than in interspace soils, growth of other plant species has been reported to be severely inhibited. Armentrout and Pieper (1988), for example, reported that the mean basal cover of grasses located directly beneath pinyon and juniper trees was 3.7% and 0.7%, respectively, while adjacent interspaces contained over 10% grass cover. Low grass cover under pinyon and juniper canopies is caused by a number of factors, including severe shading (Johnsen 1962), litter accumulation that inhibits seed germination (Jameson 1966), interception of precipitation (Gifford 1970), and allelopathy effects (Jameson 1961, Lavin et al. 1968).

Soil fungal populations and composition are related to soil properties as influenced by vegetation (Christensen 1981). Fungal populations, for example, generally increase as organic matter increases (Alexander 1977). Also, Badurowa and Badura (1967) demonstrated that the composition of litter in a given plant community is the decisive factor in determining the dominant groups of fungi. To date, only limited observations have been reported concerning the changes in the fungal community (i.e., vesicular-arbuscular endomycorrhizae) associated with plant litter under pinyon or juniper trees (Klopatek and Klopatek 1987). The objective of this study was to evaluate the quantitative and qualitative differences in the saprophytic fungal community associated with soils collected beneath pinyon and juniper canopies and to compare them with the fungal community in adjacent blue grama (*Bouteloua gracilis*)–dominated interspace soils.

MATERIALS AND METHODS

Four pinyon and four juniper trees (4–6 m in height) located just east of Santa Fe, New Mexico, were randomly selected for study in August 1989. Soil samples were collected from two of the three zones described by Armentrout and Pieper (1988); zone 1 was located beneath the tree canopy, and zone 2 was well outside the canopy. This soil area (interspace) was dominated by blue grama. At each of the eight trees, four soil subsamples were collected randomly from beneath the canopy to a depth of 15 cm with a 5-cm-diameter bucket auger. The four subsamples were mixed (composited) to represent one sample per tree. Four subsamples were also randomly collected and composited from interspace soils occurring adjacent to the tree species. Thus, a total of 16 composite samples were transported in an ice cooler back to the laboratory. At the laboratory, the samples were passed through a 2-mm sieve and stored at 4 C prior to fungal analysis. An aliquot of approximately 500 grams from each soil sample was taken for laboratory chemical (soluble Na, Ca, Mg, and K; available P; total Kjeldahl N [TKN]; organic matter [OM]; pH; and electrical conductivity [EC]) and physical (percent sand, silt, and clay) analysis at the New Mexico State University Soil and Water Testing Laboratory. All methods of chemical and physical analyses have been described previously (Fresquez and Lindemann 1983).

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Numbers of soil fungal propagules were estimated by the dilution and plating technique described by Wollum (1982). For population estimates, dilutions were plated in triplicate on rose bengal-streptomycin agar (Martin 1950) and incubated at 27 C for seven days. The numbers of fungal propagules per gram of oven-dry soil are reported. Fungal groups were isolated by placing 1 mL of a 10^{-3} dilution from a 10-g over-dry weight equivalent soil sample in a petri dish, adding cooled rose bengal-streptomycin agar, and swirling for an even distribution. Ten plates were inoculated for each composited soil sample and incubated at 27 C for seven days (Fresquez and King 1989). After incubation, a portion of every colony was transferred to a carrot agar medium by removing a portion of the agar containing hyphal tips. The colony was subcultured on a carrot agar plate to allow for maximum fruiting potential and identification. After a four-day incubation period, the colonies were identified using the taxonomic guides of Barnett and Hunter (1972), Barron (1968), Gilman (1968), and Domsch et al. (1980).

Diversity of fungi may give some insight into the physiochemical conditions of the soil environment, in terms of identifying more productive soils (Fresquez et al. 1990) and/or soils that are physiochemically stressed (Fresquez et al. 1986). Thus, the diversity of fungal groups among the treatments was estimated using Shannon's index of species diversity, H (Zar 1974):

$$H = -\sum_{i=1}^{k} p_i \log p_i$$

where p_i = the proportion of fungal group i in the sample, and k = the number of groups. The corresponding test for evenness is

$$J = H/H_{\max}$$

where $H_{\max}$ = the maximum possible diversity.

An estimate of the similarity in the fungal composition among the sample populations was calculated with Sorensen's presence community coefficient (SPCC), which was described by Mueller-Dombois and Ellenberg (1974) as

$$\mathrm{SPCC} = 200\,C/(A + B)$$

where C is the total number of groups common to two habitats, A is the total number of groups in sample A, and B is the total number of groups in sample B. If the same groups were found in both samples, then the community coefficient would be 100; if the sample had no groups in common, the coefficient would be 0.

Variations in soil chemical properties and in the populations of soil fungi between trees and adjacent interspaces were analyzed using paired t tests at the .05 level. Unpaired t tests were used to compare soil properties and fungal population means between the two tree species at the .05 level.

RESULTS AND DISCUSSION

Significantly higher fungal propagules were found in soils from beneath pinyon and juniper canopies than from interspace soils (Table 1). Other soil fungal groups, such as vesicular-arbuscular endomycorrhizae, have been reported to be higher in soils from pinyon and juniper trees than from interspace soils (Klopatek and Klopatek 1987). The higher number of soil fungal propagules from pinyon and juniper trees was probably due to differences in organic matter (OM) contents, as significantly higher soil OM levels were found under canopies of both pinyon and juniper trees than in interspace soils (Table 2).

TABLE 1. Soil fungal propagules and Sorensen's presence community coefficients associated with a pinyon-juniper plant community in New Mexico.

Soil site	Fungal propagules ($\times 10^3$)	Similarity coefficients Pinyon Understory	 Pinyon Interspace	 Juniper Understory	 Juniper Interspace
Pinyon					
understory	518a[1]A[2]		44	64	38
	(123)				
interspace	43b			35	56
	(17)				
Juniper					
understory	393y A				48
	(119)				
interspace	39z				
	(15)				

[1] Means within the same column and tree species followed by the same letter are not significantly different at the .05 level using paired *t* tests (standard deviation).

[2] Means within the same column followed by the same uppercase letter are not significantly different at the .05 level using unpaired *t* tests.

TABLE 2. Soil (sandy loam) chemical properties associated with a pinyon-juniper plant community in New Mexico.

Soil site	Soluble cations (ug g $^{-1}$) Na	 Ca	 Mg	 K	Phosphorus and nitrogen (ug g $^{-1}$) P	 NH_4-N	 NO_3-N	 TKN[1]	OM[1] (g kg $^{-1}$)	EC[1] (dS m $^{-1}$)	pH
Pinyon											
understory	6a[2]A[3]	188aA	23aA	32aA	9aA	3.7aA	9.0aA	2143aA	49aA	0.83aA	7.4aB
	(1.8)	(18.8)	(4.9)	(5.08)	(3.63)	(1.74)	(5.85)	(649)	(13.3)	(0.15)	(0.17)
interspace	12a	62b	11b	1b	3b	1.6a	5.0a	525b	14b	0.44b	7.3a
	(8.2)	(17.5)	(5.1)	(0.27)	(0.83)	(0.85)	(0.56)	(271)	(2.8)	(0.08)	(0.22)
Juniper											
understory	11yA	238yA	35yA	45yA	13yA	2.8yA	10.6yA	1989yA	49yA	1.13yA	7.8yA
	(2.8)	(24.1)	(9.5)	(3.94)	(8.50)	(1.68)	(3.82)	(300)	(4.7)	(0.21)	(0.21)
interspace	9y	76z	11z	3z	4y	2.0y	5.6y	598z	16z	0.44z	7.4z
	(4.2)	(13.6)	(2.1)	(0.86)	(0.66)	(0.67)	(0.74)	(208)	(2.5)	(0.07)	(0.16)

[1] TKN (total Kjeldahl nitrogen), OM (organic matter), EC (electrical conductivity).

[2] Means within the same column and tree species followed by the same letter are not significantly different at the .05 level using paired *t* tests (standard deviation).

[3] Means within the same column followed by the same uppercase letter are not significantly different at the .05 level using unpaired *t* tests.

Soils with high OM usually have higher fungal populations than soils with low OM concentrations (Alexander 1977). Moreover, the low fungal populations in the soil from the interspaces may be attributed not only to low OM content but also to the more severe environment at the surface of the more exposed interspaces. For example, lower amounts of plant litter mulch lead to higher amounts of exposed soil, higher surface temperatures, and lower soil moisture contents that reduce soil fungal populations (Wicklow 1973).

Other soil properties, such as Ca, Mg, K, and TKN, were significantly higher under pinyon and juniper trees than in interspace soils (Table 2). Many studies have shown that soils under pinyon and juniper canopies contain higher soil nutrient levels, including N, than soils in adjacent interspaces (Barth 1980, Tiedemann 1987, Thran and Everett 1987, Klopatek 1987). Soil NH_4-N and NO_3-N levels were higher, although not significantly different, in pinyon and juniper soils than in interspace soils. In any case, the conversion of NH_4-N to NO_3-N (nitrification) does not appear to be inhibited. These data agree with Klopatek and Klopatek (1987), who found that nitrification, despite low nitrifier counts, occurred under pinyon and juniper trees. Thus, since soil fungi were found in significantly higher populations directly under pinyon and juniper trees than in interspace soils (Table 1), and since nitrifying bacteria have been reported to be partially inhibited by allelopathic substances directly beneath pinyon and juniper canopies (Klopatek and Klopatek 1987), soil NO_3-N produced under pinyon and juniper trees as compared to interspace soils may be more a result of heterotrophic rather than autotrophic nitrification. Some soil fungi have been shown to produce significant amounts of nitrate in media containing ammonium as the sole N source (Doxtader and Alexander 1966, Doxtader and Rovira 1968).

A total of 921 fungal colonies representing 40 fungal groups were isolated and identified (Table 3). Although the interspace soils contained the lowest number of species isolated, their species diversity index, which is based on the number of species and relative density, was comparable to the pinyon and juniper data. Usually, soils that contains more OM have higher fungal populations but a lower fungal diversity than soils lower in OM (Dennis and Fresquez 1989, Fresquez et al. 1990). Soils collected from under both pinyon and juniper canopies contained significantly higher fungal populations than interspace soils. However, only the soil collected underneath pinyon trees had a lower fungal diversity index than the soil from the interspace soils.

Soil fungi isolated beneath pinyon and juniper trees were highly similar (64% of the fungi were common to the two soils) in composition (Table 1). The similarity in the types of fungi isolated between these two soils was probably a result of similar OM contents. Also, most soil chemical and physical properties were similar between these two canopy soils. Although these soils contained many fungal species in common, some fungi were associated with pinyon soils more often than juniper: *Absida* spp., *Mucor* spp, *Penicillium janthinellum*, *P. restrictum*, *Trichoderma* spp., and some *Mycelia sterilia*. *Penicillium restrictum*, *Trichoderma* spp., and *P. cyclopium* dominated the soils collected under pinyon tree canopies. In contrast, fungi that were isolated more often in soils collected underneath juniper trees included *Aspergillus nidulans*, *A. niger*, *Gliocladium* spp., *Mortierella* spp., *P. cyclopium*, *P. fasciculata*, *P. monoverticillata*, *P. nigricans*, and another unidentified *Penicillium* sp. *Penicillium monoverticillata*, *P. nigricans*, and another *Penicillium* sp. isolated from soils collected under juniper canopies were not recovered at all from pinyon soils. *Penicillium fasciculata* and *P. cyclopium* dominated the soils collected below juniper tree canopies.

Table 3. Composition and distribution of fungal groups associated with a pinyon-juniper plant community. Density of isolates was obtained from ten 1:1000 soil dilution plates.

Fungal groups	Pinyon		Juniper	
	Understory	Interspace	Understory	Interspace
Absidia				
sp. 1	7	0	1	0
sp. 2	4	0	4	0
Acremonium	0	2	1	0
Aspergillus (alutaceus)				
sp. 1	0	3	0	8
sp. 2	0	3	0	0
fumigatus	0	48	0	25
nidulans	0	0	5	0
niger	0	0	3	6
A. sp.	0	0	1	0
Beauvaria	1	0	1	0
Chaetomium	0	0	1	0
Chrysosporium	1	1	0	0
Curvularia	0	0	0	3
Fusarium				
sp. 1	3	0	3	3
sp. 2	0	5	3	16
sp. 3	2	0	0	0
sp. 4	0	8	4	3
Gliocladium	6	0	12	0
Idriella	0	1	0	0
Mortierella	0	0	2	0
Mucor	17	0	11	2
Mycelia (sterilia)				
sp. 1	1	1	2	0
sp. 2	6	1	0	0
Penicillium				
cyclopium	41	0	75	9
eupenicillium	0	24	0	0
fasciculata	12	5	81	2
frequentans	28	0	27	0
janthinellum	4	10	0	0
lilacinum	2	2	1	4
luteum	1	49	2	5
monovert	0	11	29	8
nigricans	0	0	25	0
restrictum	74	30	13	0
talaromyces	0	6	0	6
P. sp. 1	0	0	22	0
P. sp. 2	4	0	0	0
P. sp. 3	0	1	0	1
Thamnidium	3	0	2	0
Trichoderma	50	0	2	6
Unidentified	1	2	0	0
No. of isolates	268	213	333	107
No. of groups	21	20	26	16
Diversity	0.97	1.04	1.16	1.14
Evenness	0.73	0.80	0.82	0.95

The soil fungal community composition beneath pinyon and juniper tree canopies was different from that of interspace soils. Pinyon and juniper soils, for example, contained only 44% and 48%, respectively, of all species in common with the interspace soils. Soil fungal organisms isolated more often from pinyon and juniper soils than from interspace soils were *Absidia* spp., *Beauvaria* spp., *Gliocladium* spp., *Mucor* spp., *Penicillium cyclopium*, *P. fasciculata*, *P. frequentans*, *P. restrictum*, *Thamnidium* spp., and *Trichoderma* spp. Most of these fungal organisms are common soil saprophytic fungi. *Beauvaria* is an insect parasite (Moore-Landecker 1972) and is probably associated with the higher microarthropod population inhabiting the litter layer under pinyon and juniper canopies (Whitford 1987). In contrast, fungal organisms isolated more often in blue grama–dominated interspace soils than in pinyon or juniper soils were *Aspergillus alutaceus* spp., *A. fumigatus*, some *Fusarium* spp., *Penicillium luteum*, and *P. talaromyces*. *Aspergillus fumigatus* and especially *Fusarium* spp. are characteristic of grassland soils (Christensen 1981) and blue grama–dominated soils in the semiarid Southwest (Fresquez et al. 1988).

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EFFECTS OF DWARF MISTLETOE ON GROWTH AND MORTALITY OF DOUGLAS-FIR IN THE SOUTHWEST

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Abstract.—The effects of dwarf mistletoe (*Arceuthobium douglasii*) on growth and mortality of Douglas-fir (*Pseudotsuga menziesii*) were studied on 387 plots in mixed-conifer stands in three national forests in New Mexico and two in Arizona. Analyses of 8,570 trees showed that low infection ratings (dwarf mistletoe classes 1 or 2) had no significant effect on tree growth, but that losses increased markedly as infection severity increased. Average volume growth losses for trees over 10 inches in diameter were: dwarf mistletoe class 3, 10%; class 4, 25%; class 5, 45%; and class 6, 65%. Mortality of Douglas-fir in stands severely infested with dwarf mistletoe was three to four times that of healthy stands. These high losses confirm the need for silvicultural control of Douglas-fir dwarf mistletoe in the Southwest.

Dwarf mistletoes (*Arceuthobium* spp.) are the most serious disease agents in southwestern forests. They increase mortality, reduce growth of infected trees, reduce seed crops, and predispose infected trees to attack by insects and other pathogens (Hawksworth and Wiens 1972). Douglas-fir dwarf mistletoe (*A. douglasii* Engelm.) is common on Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var. *glauca* [Beissner] Franco), the most abundant and commercially valuable conifer species in southwestern mixed-conifer forests (Jones 1974). However, few quantitative data are available on the effects of this parasite on Douglas-fir in the Southwest, and current control guidelines are based primarily on research from other regions (Graham 1961, Jones 1974, Gottfried and Embry 1977).

Hawksworth and Lusher (1956) reported that on the Mescalero Apache Reservation in southern New Mexico mortality in mistletoe-infested Douglas-fir stands was almost four times that of healthy stands. In a survey of commercial forest lands in Arizona and New Mexico, Andrews and Daniels (1960) reported that the mortality rate in mistletoe-infested Douglas-fir stands was four times greater than in noninfested stands; they estimated annual mortality losses from Douglas-fir dwarf mistletoe to be between 20 and 27 million board feet. They also reported that losses due to mortality caused by the mistletoe are heavier in cutover than in virgin stands of Douglas-fir.

In ponderosa pine (*Pinus ponderosa* Laws.) volume losses from reduced growth in stands severely infested with southwestern dwarf mistletoe (*A. vaginatum* subsp. *cryptopodum* [Engelm.] Hawksw. & Wiens) have been shown to exceed mortality losses (Pearson 1950, Hawksworth 1961). Volume growth losses in mistletoe-infested Douglas-fir stands have not been quantified in the Southwest, but studies in other regions (Pierce 1960, USDA Forest Service 1962, Shea 1963, Haglund and Dooling 1972, Dooling et al. 1986, Filip and Parks 1987) have demonstrated substantial decreases in growth of severely infected Douglas-fir.

Before detailed management guidelines for Douglas-fir dwarf mistletoe control in southwestern mixed-conifer forests can be developed, information on the damage caused by the parasite is needed. Therefore, this study was initiated to provide quantitative data on growth and mortality losses associated with dwarf mistletoe on Douglas-fir in the Southwest.

Methods

In 1979, 150 rectangular, 0.2-acre plots[3] were placed in 60 stands in the Apache-Sitgreaves National Forest, Arizona (2–4 plots

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[3] Because measurements of length, area, and volume are traditionally expressed in English units in forestry, we have adopted that system here.

per stand). Dwarf mistletoe infection varied from "none" to "heavy." For each plot we recorded location, elevation, aspect, slope (to nearest 5%), slope position (upper one-sixth, intermediate two-thirds, or lower one-sixth), stand history, date disturbed (when applicable), and habitat type (Moir and Ludwig 1979). Plots were not located in stands that had been substantially disturbed in the last 12 years.

The following data were recorded for each tree greater than 4.5 feet in height:

1. Diameter at breast height (dbh) of Douglas-fir (nearest inch) and all other species (nearest 2.0 inches).
2. Height (nearest foot) and age of up to four Douglas-fir from each one-inch diameter class represented in the plot. Height (nearest 5.0 feet) for all other species in the plot.
3. Dwarf mistletoe rating (DMR, Hawksworth 1977) for all live trees and recently dead trees that could be assigned an accurate rating.[4]
4. Condition—alive or dead.
5. Radial growth (nearest 0.05 inch) at breast height for the last 10 years for three Douglas-fir from each DMR class and age class represented in the plot.
6. Height and breast height age of four to six dominant or co-dominant Douglas-fir with DMRs less than 3 and showing no signs of past suppression on increment cores for determination of Douglas-fir site index (Edminster and Jump 1976). Site index trees were selected outside the plot when necessary but were in the same stand and habitat type.

During 1980 and 1981, 237 rectangular plots were established in 40 stands (2–4 plots per stand) on the following national forests: Apache-Sitgreaves (98 plots) and Kaibab (12 plots) in Arizona, and Lincoln (57 plots), Carson (43 plots), and Santa Fe (27 plots) in New Mexico. Data-collection procedures were similar to those used in 1979 but were altered slightly to obtain data for the development of a yield-simulation model for southwestern mixed-conifer forests (Edminster and Hawksworth 1984, Edminster et al. 1990). Plots were selected using the same criteria as in 1979 except that plot size was adjusted to include at least 150 live trees greater than 4.5 feet in height. Stand data recorded for each plot were the same as in 1979. The following data were recorded for each tree greater than 4.5 feet in height in a plot: species, dbh (nearest 0.1 inch), DMR, crown class (dominant, co-dominant, intermediate, suppressed), mortality rating (dead 0–5 years, dead 6–10 years, dead over 10 years), and 10-year radial growth (nearest 0.05 inch) at breast height for trees greater than 0.5 inch dbh. In addition, height and age data were taken for the following trees: total height (nearest foot) of two or three living or dead trees from each one-inch diameter class represented for each species occurring in a plot, height (nearest foot) to base of live crown on live trees measured for total height, distance (nearest foot) from the ground to the fifth and tenth whorls from the top of the tree of live trees measured for total height, and breast height age for two live trees from each two-inch diameter class represented for each species in a plot. Selection of Douglas-fir site index trees followed the same criteria as in 1979. A total of 8,570 Douglas-fir were measured for growth during this study.

RESULTS

Nearly two-thirds of the plots (249) had more than half their total plot basal area in Douglas-fir. About one-quarter of the plots (105) had no dwarf mistletoe, and an additional one-quarter (105 plots) were lightly infested (stand DMR 0.1–1.0). The remaining plots were distributed by stand DMR as follows: 1.1–2.0, 49 plots; 2.1–3.0, 58 plots; 3.1–4.0, 49 plots; and greater than 4.0, 21 plots. One hundred seventy-four (45%) of the plots were in virgin stands and the rest in cutover areas. The distribution by time since last cutting was 12–20 years (66 plots), 21–30 years (81 plots), and more than 30 years (66 plots). Total basal area ranged from 17 to 470 square feet per acre. Douglas-fir site index ranged from 46 to 110 feet at 100 years (dbh age).

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[4] The 6-class dwarf mistletoe rating system divides the live crown of a tree into thirds, and each third is rated separately. 0 no mistletoe infection, 1 light infection, 2 heavy infection. In pines, the separation of each third into light or heavy categories is based on the percentage of branches infected (1 less than half the branches infected, 2 more than half infected). However, in Douglas-fir, because of the very small mistletoe plants and the frequent development of witches' brooms, a distinction based on a proportion of the crown volume affected by witches' brooms is more practical. Thus, if brooms occupy less than half the crown volume in a third, it is rated as 1, or 2 if more than half is occupied. The ratings for each third are totaled to obtain a dwarf mistletoe rating (DMR) for the tree. Adding the DMRs for all live trees in a stand and dividing the total by the number of trees equals the stand DMR.

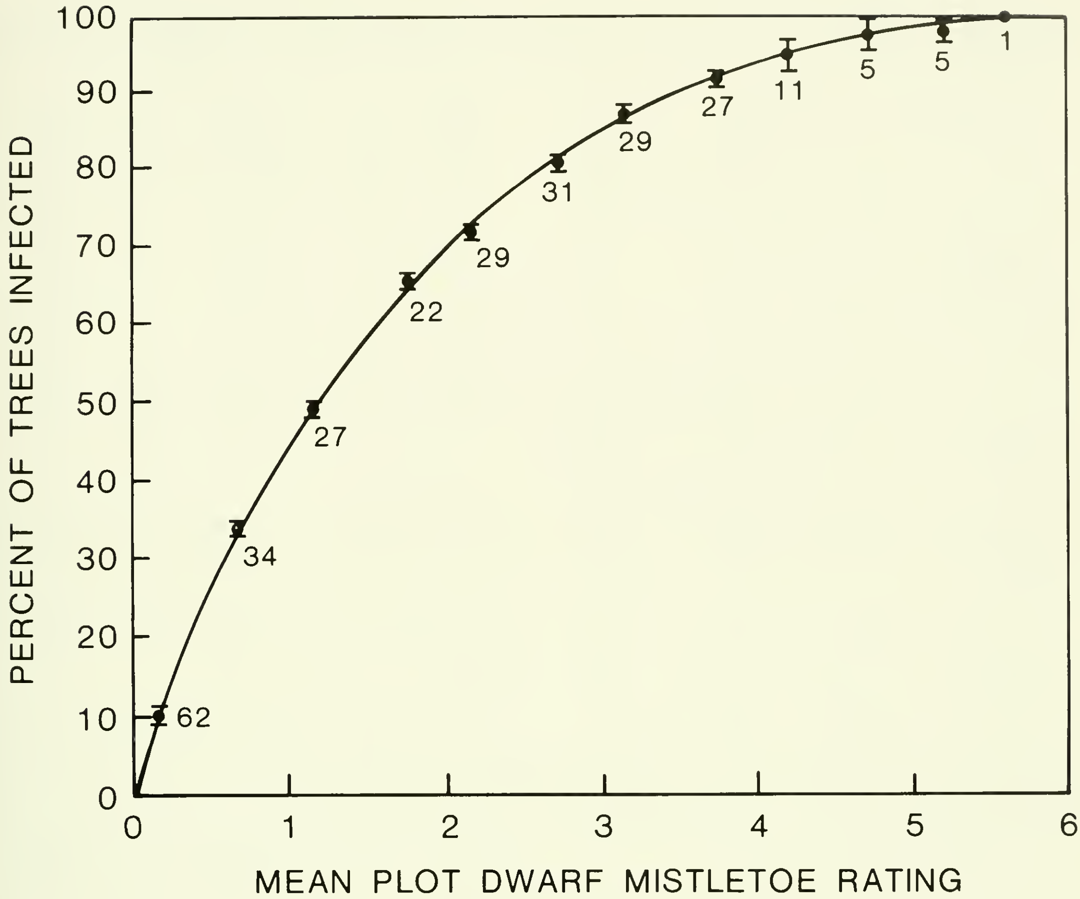

Fig. 1. Percent infection in relation to stand DMR for Douglas-fir dwarf mistletoe in southwestern mixed-conifer stands. The figures represent the number of plots in each 0.5 infection class.

TABLE 1. Ten-year radial growth for Douglas-fir by dwarf mistletoe rating (DMR) and diameter classes, and percent difference from DMR class 0.[a]

	DMR 0		DMR 1		DMR 2		DMR 3		DMR 4		DMR 5		DMR 6	
Diameter class (inches)	No. trees	Growth (inches)	No. trees	% Diff.	No. trees	% Diff.	No. trees	% Diff.	No. trees	% Diff.	No. trees	% Diff.	No. trees	% Diff.
6.1–10.0	1,612	0.32	262	+6	220	+6	271	−3	185	−28	204	−44	351	−53
10.1–16.0	1,458	0.40	269	−2	194	−5	276	−12	207	−35	272	−53	298	−65
16.1–30.00	1,009	0.42	268	0	216	0	307	−19	283	−33	262	−52	146	−69
All trees	4,079	0.37	799	+3	630	+3	854	−9	675	−30	738	−49	795	−62

[a] Includes 1979–81 data.

The relationship between percentage of trees infected and stand DMR is shown in Figure 1. No significant differences in this relationship for trees in various diameter classes could be demonstrated.

Ten-year periodic radial growth at breast height was calculated for pole-size trees (dbh 6.1–10.0 inches), small sawtimber (dbh 10.1–16.0 inches), and large sawtimber (dbh > 16.0 inches) (Table 1). Little if any effect of dwarf mistletoe was found in DMR classes 1 or 2; overall, the percent reduction was about

Table 2. Ten-year periodic annual volume increment (PAI) by dwarf mistletoe rating (DMR) and diameter class for Douglas-fir (1980 and 1981 data only).

		Diameter class (inches)		
		Poles (6.1–10.0)	Small sawtimber (10.1–16.0)	Large sawtimber (16.0+)
DMR	PAI[a]	0.11A[b]	0.35A	0.84A
0	N	1,391	1,148	699
DMR	PAI	0.12A	0.34A	0.83A
1	N[c]	166	173	134
% change		+9	−3	−1
DMR	PAI	0.12A	0.32A	0.81A
2	N	143	110	109
% change		+9	−9	−4
DMR	PAI	0.10A	0.33A	0.75B
3	N	197	172	167
% change		−9	−6	−11
DMR	PAI	0.08B	0.24B	0.67B
4	N	141	139	122
% change		−27	−31	−20
DMR	PAI	0.07B	0.18C	0.45C
5	N	148	192	140
% change		−36	−49	−46
DMR	PAI	0.05C	0.13D	0.28D
6	N	296	229	105
% change		−55	−63	−67

[a] Ten-year periodic annual increment (cubic feet/year); trees larger than 6.0 inches dbh only.

[b] Numbers followed by different letters are significantly different within each diameter class, oneway ANOVA, p .05, Student-Newman-Kuels.

[c] Percent change from DMR 0 (PAI).

Table 3. Total cubic foot volume, infected live volume, and dead volume for Douglas-fir by stand dwarf mistletoe rating (DMR) class (1980 and 1981 data only).

Stand DMR class	Number of plots	Total cubic feet/acre	Percent of live volume infected	Percent volume dead
0	105	5,590	0	1.3
0.1–0.5	68	9,130	23	2.5
0.6–1.0	37	6,630	56	2.6
1.1–1.5	20	9,060	61	2.6
1.6–2.0	29	6,660	80	3.4
2.1–2.5	26	8,830	91	3.6
2.6–3.0	32	5,300	94	4.6
3.1–3.5	27	7,680	93	5.0
3.6–4.0	22	9,560	95	4.1
>4.0	21	5,850	99	3.8

10% for DMR class 3, 30% for class 4, 50% for class 5, and 60% for class 6.

Ten-year periodic annual (cubic) volume increment (Hann and Bare 1978) was determined by DMR class for pole-size trees (diameter ranges as above), small sawtimber, and large sawtimber size classes (Table 2). Percent change in 10-year periodic annual volume increment shows a pattern similar to that for 10-year periodic radial growth. Much variation was encountered for all size classes in DMR classes 1 and 2 but much less in classes 3–6. Class 3, 4, 5, and 6 trees had decreases in periodic annual volume of 6–11%, 20–31%, 36–49%, and 55–67%, respectively, when compared with the growth of healthy trees of the same size classes (Table 2). However, when a one-way analysis of variance ($p = .05$, Student-Newman-Kuels) was applied to the results, only large sawtimber-size trees with DMR greater than 2 and trees with DMR greater than 3 for the smaller size classes had statistically significant volume growth reductions when compared with the growth of healthy trees (Table 2). Percent reductions in 10-year periodic annual volume increment for all sawtimber-size trees averaged approximately 10%, 25%, 45%, and 65% for infection classes 3, 4, 5, and 6, respectively.

Although site index affected the rate of 10-year periodic annual volume increment (lower sites had lower growth rates), the reductions in volume increment associated with dwarf mistletoe infection followed the same pattern as above regardless of the site index class considered. Consistent differences in the growth loss patterns associated with dwarf mistletoe infection have been demonstrated for different habitat types using the data collected in this study (Mathiasen and Blake 1984). However, no differences in growth loss could be associated with other stand attributes such as slope, aspect, or elevation based on these data.

Total cubic volume, infected live volume, and dead volume were calculated for trees larger than 6.0 inches dbh by stand DMR classes (Table 3). The volume of dead trees doubled in plots with stand DMR of 0.1–1.5 and was two and one-half to almost four times greater in plots with stand DMR greater than 1.5 when compared with the percentage of dead volume in healthy plots.

Percent mortality was calculated for the following size classes: small saplings (dbh 0.1–1.0 inch), large saplings (dbh 1.1–6.0 inches), poles, small sawtimber, and large sawtimber (diameter ranges as above) by stand DMR classes (Table 4). Percent mortality ranged

TABLE 4. Percent mortality of Douglas-fir by stand dwarf mistletoe rating (DMR) and diameter class.

Stand DMR class	Diameter class (inches)				
	Seedlings (0.1–1.0)	Saplings (1.1–6.0)	Poles (6.1–10.0)	Small sawtimber (10.1–16.0)	Large sawtimber (16.0+)
0	7	12	6	2	3
0.1–1.0	10	19	10	5	3
1.1–2.0	6	17	13	7	5
2.1–3.0	18	26	16	14	12
3.1–4.0	19	30	15	13	21
4.0+	24	44	35	22	16
All plots	10	20	12	8	6

TABLE 5. Percent mortality by stand history and diameter class for Douglas-fir.

Stand history	Diameter class (inches)				
	0.1–1.0	1.1–6.0	6.1–10.0	10.1–16.0	16.0+
Cutover (years)					
12–20	5	17	15	9	4
21–30	5	19	9	4	3
>30	15	18	10	6	10
Virgin	11	23	15	10	8

TABLE 6. Percentage of dead Douglas-fir with dwarf mistletoe ratings 0 and 2–6 by diameter class.[a]

Diameter class (inches)	Total dead trees	Dwarf mistletoe rating					
		0[b]	2	3	4	5	6
		Percentage of dead Douglas-fir					
0.1–1.0	443	70	4	4	7	3	12
1.1–5.0	1,238	68	3	3	6	5	15
5.1–10.0	354	58	1	2	6	12	21
10.1–16.0	227	49	1	1	9	14	26
16.0+	125	63	1	1	11	15	9
Total	2,387	65	3	3	7	7	15

[a] Does not include dwarf mistletoe ratings of 1 because this class included dead trees that could not be assigned an accurate rating. Trees with any indication of past mistletoe infection that could not be accurately rated were assigned a 1 to indicate they had been infected.

[b] May include infected old dead trees not having signs of past dwarf mistletoe infection. This category includes any mortality observed in plots that was probably not related to mistletoe infection.

from 1.3% to 5.0% but generally increased as stand DMR increased, particularly when the stand DMR was greater than 2.0. Mortality of small sawtimber demonstrated the largest increase in percent mortality as stand DMR increased (from 2% in healthy plots to 22% in plots with a stand DMR greater than 4.0). The percentage of dead trees was greatest for large saplings, compared with other size classes, in all stand DMR classes.

Mortality in most size classes was generally greatest in virgin stands compared to cutover stands (Table 5), but mortality in stands cutover more than 30 years prior to data collection was higher than in virgin stands for the small sapling and large sawtimber-size classes.

Forty-three percent of the dead Douglas-fir that could be accurately assigned a dwarf mistletoe rating were rated as class 6 (Table 6). Most infected dead trees in each size class were rated as class 6 except for the large sawtimber, where a higher percentage of dead Douglas-fir were rated as class 5. More dead trees in the small and large sapling-size classes were rated as class 4 than class 5. The percentage of dead Douglas-fir rated as classes 2 and 3 decreased as size class increased (Table 6).

Discussion

The relationship between percentage of trees infected and stand DMR is similar to that reported for stands infected with lodgepole pine dwarf mistletoe (*A. americanum* Nutt. ex Engelm.) (Hawksworth 1978).

Severe dwarf mistletoe infection greatly reduces volume increment of Douglas-fir in the Southwest. Ten-year annual radial growth reductions for trees in DMR classes 3, 4, 5, and 6 averaged about 10%, 30%, 50%, and 60%, respectively. Statistically significant growth losses occur for sawtimber-size trees with infection levels greater than 3. Pierce (1960) in western Montana and Shea (1963) in Oregon also showed that growth rates of severely infected Douglas-fir were markedly reduced. In addition, Filip et al. (1990) found significant reductions in 10-year mean diameter increment in dwarf mistletoe–infested Douglas-fir stands in eastern Oregon and Washington. Wicker and Hawksworth (1988) gave general loss estimates for growth reduction for all dwarf mistletoes as about 10%, 25%, and 50% or more for trees in classes 4, 5, and 6, respectively. However, our results indicate that growth reductions for Douglas-fir in the Southwest are greater than these general estimates.

Our estimates of mortality in Douglas-fir dwarf mistletoe–infested stands are similar to those reported in the Southwest by Hawksworth and Lusher (1956) and Andrews and Daniels (1960). Although not tested statistically, mortality was generally higher in mistletoe-infested virgin stands than in cutover stands in this study. Hawksworth and Lusher (1956) reported similar findings for Douglas-fir stands in southern New Mexico, but Andrews and Daniels (1960) found higher mortality rates in cutover stands. Increases in mortality are generally related to increases in stand DMR. Mortality was highest for large saplings in each stand DMR class. The reasons for the higher mortality rate in the large sapling class are unknown, but they may be related to more severe competition for light, moisture, and nutrients, combined with increased stress related to mistletoe infection. Small saplings are subjected to severe competition, too, but usually have lower levels of mistletoe infection (Mathiasen 1986). The high mortality rates we observed in class 4 and 5 trees for Douglas-fir are in contrast to mortality patterns in mistletoe-infected ponderosa pines, where mortality is predominantly in class 6 trees (Hawksworth and Lusher 1956).

Douglas-fir dwarf mistletoe is widespread and common in southwestern mixed-conifer forests (Andrews and Daniels 1960, Hawksworth and Wiens 1972, Jones 1974, Gottfried and Embry 1977). This study demonstrates that the damage caused by Douglas-fir dwarf mistletoe in unmanaged forests can be significant in terms of increased mortality and reduced growth of Douglas-fir in heavily infested stands. Therefore, reducing population levels of this parasite through silvicultural management should be a high priority for resource managers in the Southwest.

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USING THE ORIGINAL LAND SURVEY NOTES TO RECONSTRUCT PRESETTLEMENT LANDSCAPES IN THE AMERICAN WEST

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ABSTRACT.—Rectangular surveys completed between 1796 and 1925 by the General Land Office have frequently been used in the eastern and central U.S. to determine land cover prior to European settlement. These survey notes are less often used in the western U.S., although they are the only site-specific presettlement records available in many areas. Recent efforts to restore riparian and grassland habitats require an understanding of the conditions of these sites before settlement. General Land Office Survey notes provide a description of each township, including water supplies, timber resources, and agricultural potential. The width and course of rivers and streams were recorded on survey lines, along with notes on topography, vegetation, wetlands, mineral deposits, and soils. The township and section descriptions may be used with other historic information to reconstruct presettlement landscapes. Incomplete or vague descriptions, land use before survey, bias in recording data, and contract fraud limit the usefulness of some survey notes. However, survey notes have proved useful in establishing baseline conditions of riparian habitats in Colorado and Oregon and grasslands in Colorado and New Mexico.

Information from historic photographs, expedition journals, and original land survey notes have been used to reconstruct vegetation at the time of European settlement (Hutchison 1988, Noss 1984). The General Land Office (GLO) notes have been considered the most reliable source of historic landscape data because of standardized data collection and systematic coverage of most of the United States (e.g., Bourdo 1956). Many of the published studies using survey notes described regional patterns in upland forests of the north central and northeast U.S. (e.g., Grimm 1984, Cottam 1949). Land survey notes have been used to assist in determining fire return intervals (Lorimer 1977), to substantiate early explorers' records (Grimm 1984, Rankin and Davis 1971), and to assess range trends (Buffington and Herbal 1965). Few studies have used earlier metes and bounds survey notes available in the eastern states for vegetation characterization because of the lack of standardized data (Siccama 1971). Use of survey notes for site-specific studies, especially in the landscape of the American West, has not been evaluated. This review discusses the methods used by field survey crews, limitations of interpreting survey data, and site-specific applications in the western U.S.

GENERAL LAND OFFICE SURVEYS

Surveys east of Ohio were conducted at the local political level and did not use standardized techniques (Siccama 1971). The rectangular survey was initiated at the western boundary of Pennsylvania when the Land Ordinance of 1785 was passed by Congress. The Northwest Ordinance of 1787 encouraged the rapid settlement of new territories and states, creating the need for surveys. The Office of Surveyor General was created by the Land Act of 1796, when public lands were offered for disposal and further escalated the need for surveys. Several configurations of the rectangular survey were used between 1785 and 1796. Eventually the survey was standardized to partition the land into townships of thirty-six square miles that included one-mile-square sections (Fig. 1). Townships were aligned along north-south principal meridians and east-west baselines.

The General Land Office was formed in 1812 to oversee the national survey. Surveys were contracted to the lowest bidder until 1908 (Senti 1988, personal communication), the surveyor being compensated for each mile of line completed while also being accountable for errors in the survey. The contract holder hired the survey crew. Although each

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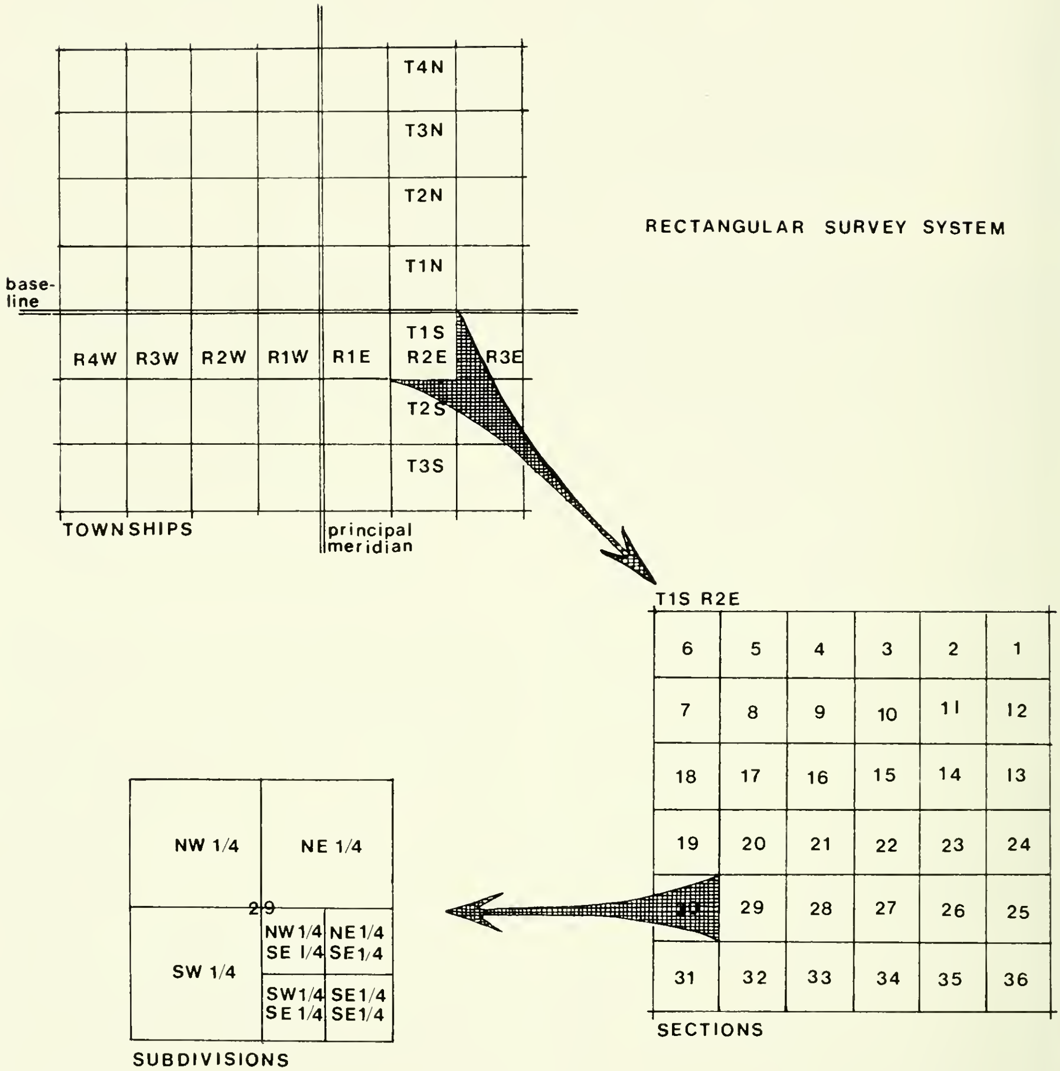
RECTANGULAR SURVEY SYSTEM
T4N
T3N
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base-line
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R3W
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R3E
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T3S
TOWNSHIPS
principal meridian
T1S R2E
6 5 4 3 2 1
7 8 9 10 11 12
18 17 16 15 14 13
19 20 21 22 23 24
30 29 28 27 26 25
31 32 33 34 35 36
SECTIONS
NW 1/4
NE 1/4
29
SW 1/4
NW 1/4 SE 1/4
NE 1/4 SE 1/4
SW 1/4 SE 1/4
SE 1/4 SE 1/4
SUBDIVISIONS

Fig. 1. The rectangular survey partitioned land into townships of thirty-six square miles that included one-mile-square sections. Section subdivisions were generally not surveyed during the original fieldwork.

crew member and the surveyor took oaths to perform their duties faithfully (Cazier 1976), frequent fraudulent surveys caused the General Land Office to abandon contracting in 1908. Since 1908, salaried federal employees have conducted the surveys.

The surveys notes were transfered to each state as the survey was completed, but records for states with incomplete surveys in 1925 were retained by the General Land Office. The Office of Surveyor General was abolished in 1925 when most of the suitable public land had been surveyed, and duties were then reassigned within the General Land Offices. However, some remote areas were not surveyed by that time. In addition, privately held Spanish Land Grants, common in the southwestern U.S., were never part of the public domain lands of the United States and were not included in the rectangular survey system. Areas rich in locatable minerals, such as gold, silver, and lead, were usually not suitable for agricultural use and often were not surveyed in the rectangular survey system. Mining claims could be located on mineral deposits under the General Mining Law of

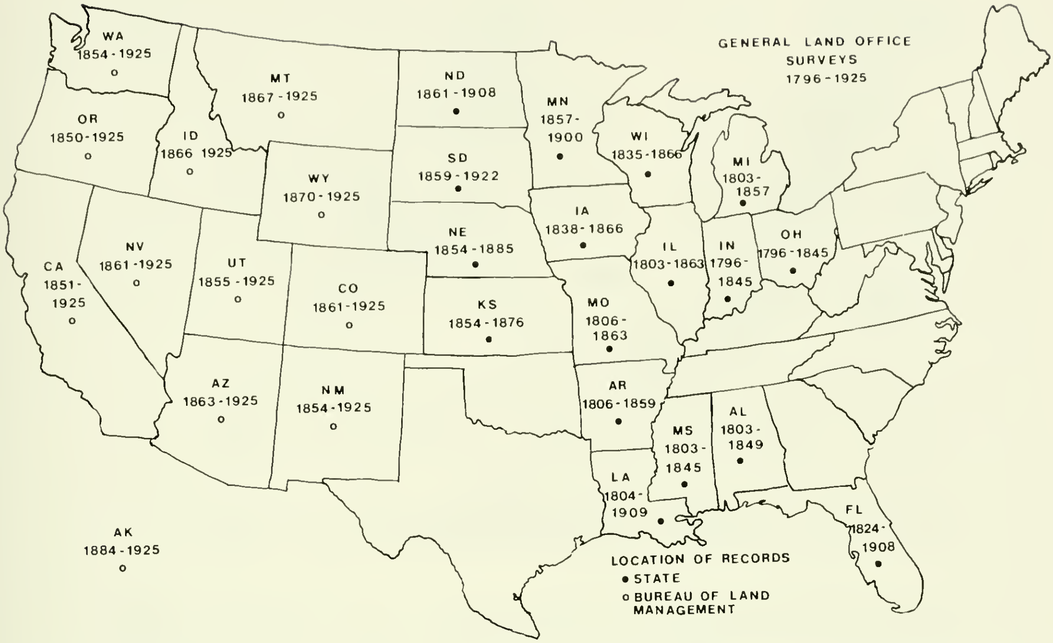

GENERAL LAND OFFICE SURVEYS 1796-1925
WA 1854-1925 o
OR 1850-1925 o
ID 1866 1925 o
MT 1867-1925 o
ND 1861-1908 •
SD 1859-1922 •
MN 1857-1900 •
WI 1835-1866 •
MI 1803-1857 •
WY 1870-1925 o
NE 1854-1885 •
IA 1838-1866 •
IL 1803-1863 •
IN 1796-1845 •
OH 1796-1845 •
CA 1851-1925 o
NV 1861-1925 o
UT 1855-1925 o
CO 1861-1925 o
KS 1854-1876 •
MO 1806-1863 •
AZ 1863-1925 o
NM 1854-1925 o
AR 1806-1859 •
MS 1803-1845 •
AL 1803-1849 •
LA 1804-1909 •
FL 1824-1908 •
AK 1884-1925 o
LOCATION OF RECORDS
• STATE
o BUREAU OF LAND MANAGEMENT

Fig. 2. The dates of the original land survey and location of field notes are listed for each state included in the General Land Office Surveys. The original colonies and Tennessee were surveyed prior to the rectangular surveys. Texas was not a public land state when admitted to the union. Data from White (1984).

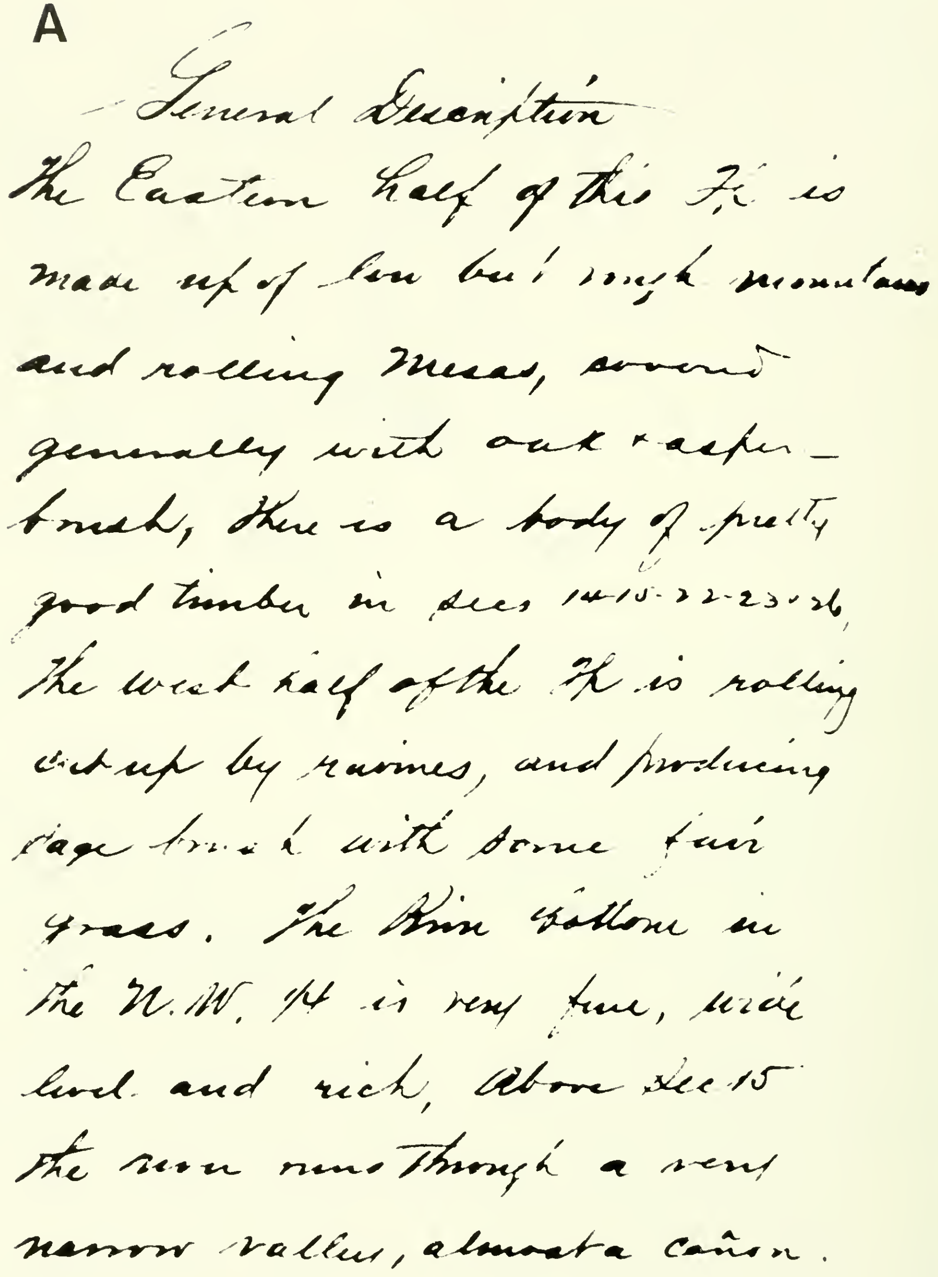
1872. The mining claimant had to obtain an engineering survey of the claim to obtain a patent (deed). The field notes of these surveys often contain useful information, particularly in timbered areas where bearing trees were marked.

The Taylor Grazing Act of 1934 closed all unappropriated land to settlement and formed the Grazing Service. In 1946 the Grazing Service and the General Land Office were merged to form the Bureau of Land Management. Public land surveys are now conducted by the Branch of Cadastral Survey of Bureau of Land Management state offices. Figure 2 lists the dates of the survey and location of records for each state. Records are available for public use in state government offices or in Bureau of Land Management state and district offices.

Data recording evolved during the General Land Office Survey. At least twenty versions of the general instructions to surveyors were issued from 1804 to 1902 (White 1984). Outer township lines were always surveyed first, followed by section lines, usually starting at the southeast corner of the township and progressing east to west and south to north. Distances were measured in chains: 1 chain = 100 links (66 feet), 1 mile = 80 chains (5,280 feet), 1 acre = 10 sq. chains (43,560 sq. feet). The width and course of rivers and streams were recorded where the surveyed section lines crossed them. Notes on topography, timber and undergrowth, swamps, ponds, stone quarries, coal beds, mineral deposits, and fossil locations were also recorded. Later field notes also included descriptions of nearby settlements and roads. Figures 3A–C represent a sequence from the Yampa River in Routt County, Colorado, including a general township description, map from the 1877 survey, and map from a 1913 resurvey of the same area.

VEGETATION.—After 1830, surveyors were instructed to map "prairies and swamps" with separate symbols on maps accompanying the field notes. Surveys after 1842 include a general description of the township following the survey notes. "Quality" of the soil for cultivation was categorized first rate, second rate, third rate, and unfit for cultivation. These categories appeared in some survey notes before 1843. These soil categories were never defined and should be considered relative.

A



General Description
The Eastern half of this Tp. is
made up of low but rough mountains
and rolling Mesas, covered
generally with oak & aspen-
brush, there is a body of pretty
good timber in secs 14-15-22-23-26,
The west half of the Tp is rolling
cut up by ravines, and producing
sage brush with some fair
grass. The River bottom in
the N.W. 1/4 is very fine, wide
level and rich, Above sec 15
the river runs through a very
narrow valley, almost a cañon.

Fig. 3A. General description of township including the Yampa River site.

For example, "second rate" soil in the Midwest may indicate something quite different from a "second rate" soil in the arid West. The description also was to include a list of tree species in descending order of abundance (Bourdo 1956). Recording the distance along a section line after leaving a river or creek bottom, prairie, swamp, grove, or windfall was required by instructions used after 1845. By 1850 the kinds of grasses and herbage present were required in the general description.

HYDROLOGY.—Water quality (fresh, saline,

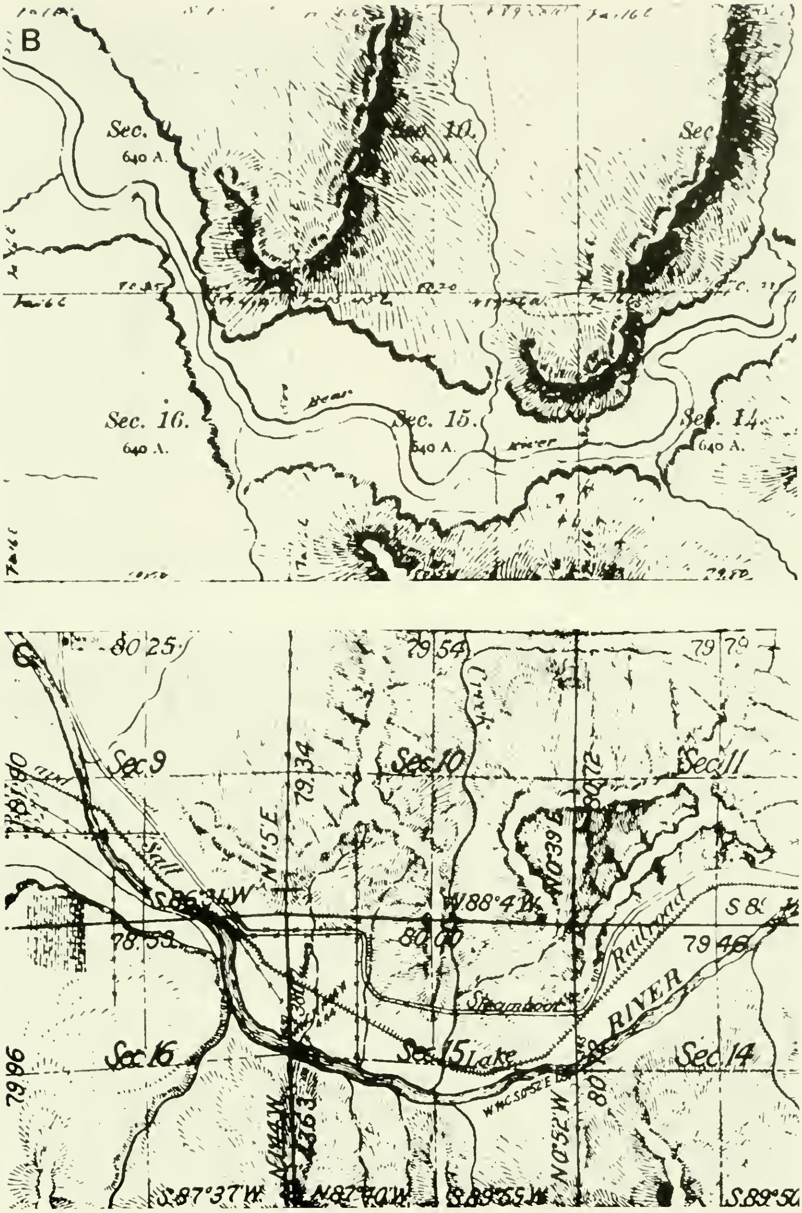

B
Sec. 9
640 A.
Sec. 10.
640 A.
Sec.
Sec. 16.
640 A.
Bear
Sec. 15.
640 A.
river
Sec. 14.
640 A.
C
80 25
79 54
79 79
Sec 9
Sec 10
Sec 11
79.34
N1°5'E
Salt
S86°2'W
N88°4'W
80.00
N0°39'E
80.12
78.53
79.46
Railroad
S 8
RIVER
Steamboat
Sec 16
Sec 15
Lake
Sec 14
79.96
79.81
N0°52'W
80
S87°37'W
N87°40'W
S89°55'W
S89°50

Fig. 3B and 3C. Survey map from the field notes of 1877 (Fig. 3B) for the Yampa River site. Survey map from the field notes of 1913 (Fig. 3C) for the Yampa River site. Note the alignment of the river in Section 15 on this map compared with the 1877 map. The positions of river crossings were accurately located along section lines, but the courses of rivers within sections were estimated.

or mineral) for all streams, lakes, ponds, and springs was also described after 1845. The quantity, location, and depth of inundation were recorded for "swamp and overflow" lands in states affected by the "Swamp Acts" of 1849, 1850, and 1860 (Cazier 1976). Swamp Acts granted states or territories title to wetland areas over forty acres to assist in reclaiming lands for agriculture. States affected by Swamp Acts were Alabama, Arkansas, California, Florida, Illinois, Indiana, Iowa, Louisiana, Michigan, Minnesota, Missouri, Ohio, Oregon, and Wisconsin. In other states, wetlands and streams were only located as section lines crossed them and estimated in the interior of sections (see Figs. 3B–C).

WITNESS TREES.—In forested areas, witness and bearing trees were blazed at every mile and half mile. In most surveys the terms "witness trees" and "bearing trees" were used interchangeably. Two or four trees were marked at section corners, and two were marked at quarter sections at the half-mile point along section lines. In addition, section corners were marked with mounds, rock monuments, charred wooden stakes, or a combination of these, along with pits dug in the ground until 1908. Brass caps have marked corners since 1908. The common name of the tree and its diameter were also recorded. Bearing trees were distinguished from witness trees (Bourdo 1956). Unlike bearing trees, the distance and direction to witness trees were not required information. The common names and diameters of trees along section lines were also noted.

LIMITATIONS

Some limitations exist for use of land survey notes, in addition to the lack of coverage for some states, private land grants, and remote areas. Inconsistent descriptions, land use before surveys, bias and error in vegetation descriptions, and fraudulent surveys may restrict the use of land survey notes for characterizing natural vegetation. In addition, some notes are difficult to read because of illegible handwriting or poor microfiche reproductions of light handwriting.

INCONSISTENT DESCRIPTIONS.—Survey instructions standardized data collection for each state or region, but inconsistencies still existed between survey crews. Further, special instructions were often issued to field crews that may have modified general guidelines (White 1984). The detail of landscape description varies greatly between notes. Some surveyors would fully describe the soils, vegetation, landforms, and potential land use, whereas others would restrict comments to topography and a general land use statement. For example, survey notes were reviewed to determine whether active sand dunes near the Mississippi River in Minnesota originated from grazing and cultivation or were present prior to settlement (Galatowitsch 1984). Field notes from 1855 did not mention active dunes, only a "third rate" sandy prairie. However, since little detail was available throughout the surveyor's notes, no inference could be made concerning the origin of the dunes from the account.

LAND USE BEFORE SURVEYS.—The land surveys were not conducted before European settlement in some regions. New Mexico, for example, had been inhabited by the Spanish for nearly 300 years before the surveys of the late 1800s and early 1900s. A survey near Santa Fe, New Mexico (Gross 1973), noted in a general township description of 1919:

> . . . across the SW corner cuts the Denver and Rio Grande railroad. Bordering the railroad, approximately, is the wagon road leading to Antonito, Colo. . . . The nearest post office and store is at Tres Piedras, on the railroad, three miles to the NW of the NW corner.

Gross (1973) was trying to characterize "pristine rangeland vegetation" in northwestern New Mexico from land survey notes. In addition to the effects of early Spanish settlement, much of the area had been influenced by the Anasazi until 1000 years before present and by other Native American cultures since. Overutilization of natural resources, primarily woodland vegetation, has been theorized as a cause of the collapse of the Anasazi society (Betancourt and van Devender 1981). If the landscape was radically modified, the original land survey notes can only represent data from a point in time rather than a "pristine baseline." The effects of pre-European land use should be considered in many parts of the western U.S.

BIAS IN VEGETATION DESCRIPTION.—Bias in field notes for forest studies has been well documented. Bearing trees were selected to be easily relocated, not necessarily the closest to the section or half-section post. Bearing trees were selected by size, age, species longevity, distance from the corner, and conspicuousness (Grimm 1984). Statistical analysis of quantitative tree data from the field notes is flawed because certain sizes and species were favored and because the sample is systematic, not random (Grimm 1984). Bias in vegetation descriptions of nonforested habitats is difficult to assess. General instructions to surveyors required information on available forage; thus, descriptions of shrubs and forbs may be underrepresented.

ERRORS IN SPECIES IDENTIFICATION.—Species identifications are not standardized among surveys. For example, "bunch grass"

TABLE 1. Plant names used in the territorial survey of New Mexico (Gross 1973).

Name used in 1880	Common name today	Scientific name
Buffalo grass	Buffalo grass	*Buchloe dactyloides*
Bunch grass		
Grama grass	Blue grama	*Bouteloua gracilis*
Sand grass		
Salt grass	Salt grass	*Distichlis stricta*
Buckbrush	Deer brier	*Ceanothus fendleri*
Chamiza	Four-wing saltbrush	*Atriplex canescens*
Chico	Iodine bush	*Allenrolfea occidentalis*
Greasewood	Greasewood	*Sarcobatus vermiculatus*
Labina		
Locust	Locust	*Robinia neomexicana*
Manzanita		*Arctostaphylos* sp.
Sabinos		
Sage	Sage	*Artemisia tridentata*
Cedar	Juniper	*Juniperus* spp.
Oak	Gambel's oak	*Quercus gambelii*
Pine	Ponderosa pine	*Pinus ponderosa*
Piñon	Piñon	*Pinus edulis*

most likely refers to tall- and mid-grass prairie species such as *Andropogon* spp., *Sorghastrum nutans*, and *Panicum virgatum* in the Great Plains. Gross (1973) developed an equivalency table to interpret land survey data from New Mexico (Table 1). Grimm (1984) also developed an equivalency table for the Big Woods of Minnesota. "Soft maple" appears to refer to *Acer saccharinum* and *Acer rubrum;* "sugar maple" is *Acer saccharum*. White ash is assumed to be *Fraxinus pennsylvanica* since the study area is not within the range of *Fraxinus americana*. *Quercus borealis* and *Quercus ellipsoidalis* were variously categorized as "black oak" and "jack oak," probably based on size.

SURVEY CONTRACT FRAUD.—Fraud with surveying contracts, most notably the Benson Syndicate, resulted in fictitious records being substituted for survey data. Fraudulent surveys were most common in California and other western states during the 1870s and 1880s (Cazier 1976). Fraud ranged from estimating some entries within a township to fabricating entire records. Some contracts that were not deliberately fraudulent compromised accuracy in areas deemed by the survey as unsuitable for agricultural purposes. For example, a mountain valley thought by the surveyor to be suitable for agriculture would be accurately located within a township, and the description and location of adjacent rough terrain would be estimated (Senti 1988, personal communication). Although surveys before 1880 are considered reliable in Colorado, as much as 15% of the land in the state may not have actually been surveyed. Figures 4A–B compare a fictitious survey map from 1889 in the Wolf Creek Pass area, Colorado, with the USGS 7.5′-series topographic map of the area. The extensive fraud of the late 1800s was eliminated after 1908, when surveys were no longer contracted. Distinctive features may be present to confirm the accuracy of a survey entry. In an area southwest of Denver, distance and direction to a sandstone ledge with a small spring were included in the field notes. Colorado Natural Areas Program staff located the no-longer flowing spring, confirming the reliability of the survey for that area.

APPLICATIONS

RIPARIAN HABITAT RESTORATION.—Despite limitations of interpreting land survey data, this historic reference is the only record available at settlement for many site-specific studies. Riparian habitat restoration is a focus in the West because of degradation from livestock grazing and logging and hydrologic modification from water development and urbanization. Survey notes have been used to assess changes and establish restoration goals in some riparian areas. Sedell and Frogett (1984) compiled information on the position of river channels and distribution of riparian forests of the Willamette River in western Oregon. Most of the area was not yet homesteaded at the time of the survey during the 1850s. The U.S. Army Corps of Engineers

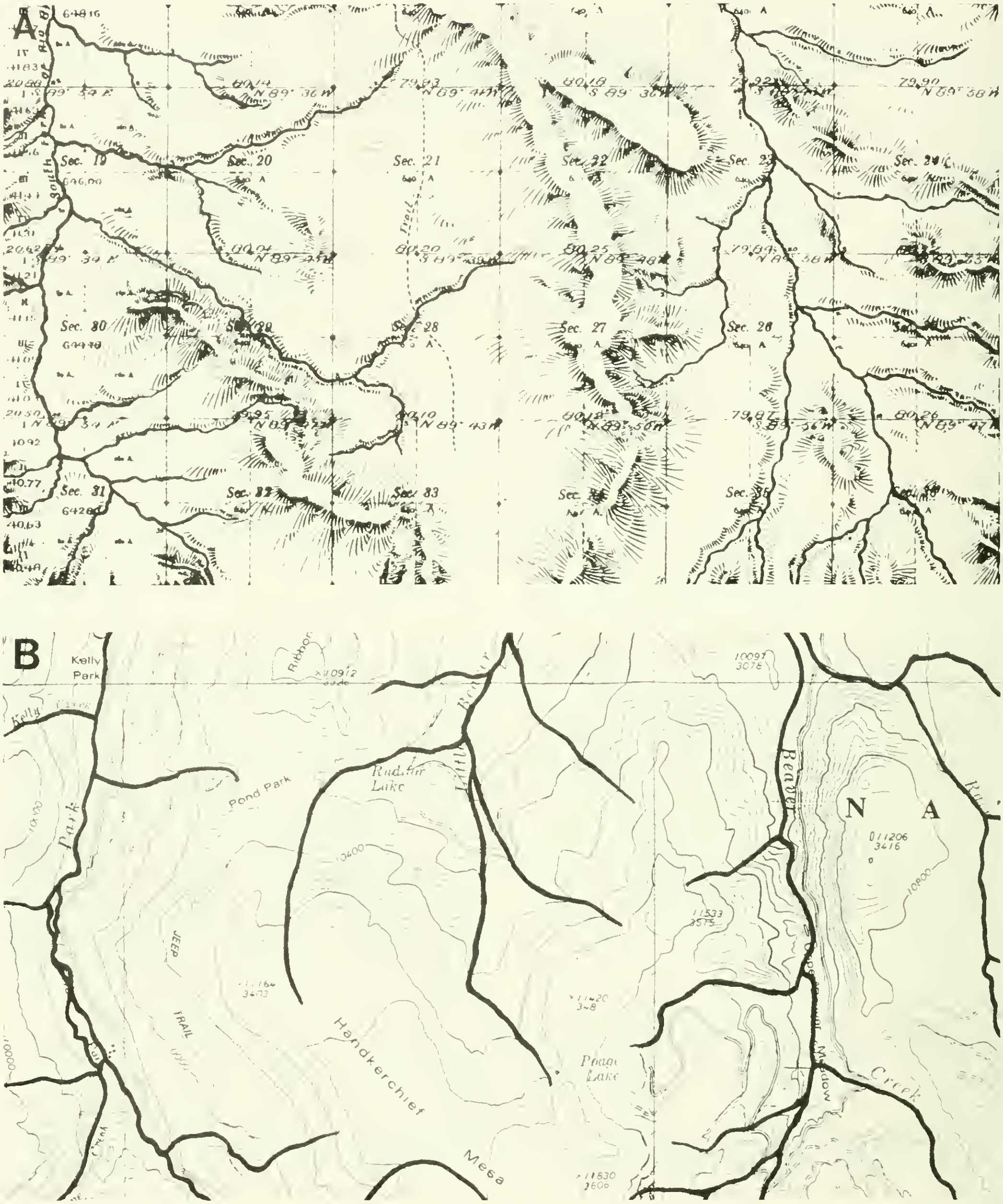

A
Sec. 19
Sec. 20
Sec. 21
Sec. 22
Sec. 23
Sec. 24
Sec. 30
Sec. 29
Sec. 28
Sec. 27
Sec. 26
Sec. 25
Sec. 31
Sec. 32
Sec. 33
Sec. 34
Sec. 35
Sec. 36
Trail
B
Kelly Park
Kelly Creek
Park
Pond Park
Rudolfo Lake
Beaver
N A
JEEP TRAIL
Handkerchief Mesa
Poage Lake
Meadow
Creek
Little Beaver

Fig. 4A and 4B. Figure 4A depicts an area in the vicinity of Wolf Creek Pass, Colorado (south portion of Township 38 North, Range 3 East of the New Mexico Principal Meridian), from survey notes of 1881. Compare this map with the USGS map of the same area from 1978 (Fig. 4B) and note the lack of agreement of stream locations. The positions of stream crossings along township lines are generally accurate, but the courses of streams within the township are fictitious. Apparently, township lines were actually surveyed, but interior section lines were not.

began snag removal from the river in 1868. Species composition of the forest has not changed since the survey: dominant species are Douglas fir (*Pseudotsuga menziesii*), Oregon white ash (*Fraxinus oregana*), cottonwood (*Populus trichocarpa*), willow (*Salix* spp.), alder (*Alnus rubra*), and big leaf maple (*Acer macrophyllum*). However, the Willamette River once consisted of multiple channels, filled with snags and fallen trees. Snag removal and wing dam construction to facilitate navigation confined the river to one channel. Clear-cutting at settlement reduced the riparian forest that extended 1.5–3 km on either side of the river to a narrow ribbon along the channel. The changes in the Willamette River have resulted in a fourfold decrease in river shoreline and a loss of habitat diversity for aquatic animals.

Savonen (1985) investigated the feasibility of restoring West Bijou Creek in northeastern Colorado. Unlike many other streams in the Great Plains of Colorado, West Bijou Creek has a natural water regime: natural flooding, deposition, and erosion still occur. The original land surveys in 1866 and 1867 describe an area in the valley of West Bijou Creek as "good grass . . . good hayland on the creek bottom . . . creek bottom covered with good growth of grasses." The soil was characterized as "first rate, good for agriculture." Surveyors recorded the presence of cottonwood (*Populus deltoides*) and box elder (*Acer negundo*) along the creek 35 miles downstream from the headwaters. Willow (*Salix amygdaloides* and *S. exigua*) must have been present occasionally since surveyors "set a charred willow stake" in some places to mark sections and half sections near the creek. No other mention of timber was made. The dominant species have not changed, although wooded areas are more extensive. Records from the Colorado Historical Society substantiate the soil description for the West Bijou Creek valley made by the surveyors. In 1888 the soil in the valley was described as "dark, rich, brown and black sandy loam and is very deep. . . . It is as nearly inexhaustible as any known soil." Much of the area was subsequently cultivated and supported small grains, corn, onions, and cabbage without irrigation. The drought and dust storms of the 1930s resulted in severe erosion. The exposed soil adjacent to the floodplain is now clayey and has been converted to rangeland. Although "bunch grasses" and "buffalo grass" were noted for adjacent uplands, the surveyors did not describe the species in the West Bijou Creek floodplain. The survey notes suggest that the riparian community has switched dominance from grasses to trees. Restoration of riparian areas along West Bijou Creek will be potentially difficult because of the loss of topsoil.

A riparian restoration was proposed for Tollgate Creek at the Plains Conservation Center, southeast of Denver. Several mature cottonwood trees (*Populus deltoides*) exist along the dry creek near an area intensively used by livestock since settlement. Land survey notes from 1865 were used by the Colorado Natural Areas Program to assess whether Tollgate Creek was a forested stream or a grassland draw before settlement. The 1865 survey indicated that although the area had not yet been settled, open-range livestock use may have occurred on this site. Tollgate Creek crosses section lines in eight places in the vicinity of the proposed restoration. At all eight locations Tollgate Creek was described as a dry ravine with clay soil. The surveyor described the township as "unsuitable for farming because of the lack of running water." Unlike Tollgate Creek, where no reference to timber was made, the same surveyor described Coal Creek, a nearby stream, as "well-timbered with cottonwood . . . and never dry." The survey notes demonstrate that Tollgate Creek is a naturally intermittent stream and suggest that a riparian grassland, not a cottonwood riparian forest, should be restored.

GRASSLAND RESTORATION.—Grasslands have been a focus of restoration efforts because of agricultural conversion and effects of overgrazing. Vegetation changes on the Jornada Plain of New Mexico were described by Buffington and Herbel (1965) based on data from the land survey of 1858. Increases in three shrub species, creosotebush (*Larrea tridentata*), mesquite (*Prosopis glandulosa*), and tarbush (*Flourensia cernua*), appeared to occur when overgrazing reduced grass cover. Eight categories were established, based on combinations of the species recorded in the survey notes. Abundance of shrubs was based on surveyors' use of the words *few*, *some*, and *abundant*. A vegetation map was constructed based on shrub species distribution and abundance. Reconnaissance range surveys of the area were conducted in 1915, 1928, and 1963. Maps were constructed for each data set by applying the same criteria to information from later surveys. "Good grass" was dominant on more than 90% of the study area in 1858. By 1963, "good grass" covered only 25% of the Jornada Plain. Mesquite invaded sandy sites, spreading from areas around stock water developments. Creosotebush occurred in low abundance with grass in 1858. Areas dominated by creosotebush increased from about one section (640 acres) in 1858 to over 12,000 acres in 1963.

Bonny Prairie is a mixed-grass prairie dominated by little bluestem (*Andropogon scoparius*) in extreme east central Colorado. The prairie occurs on loess deposits on the summit and gentle side slopes of hills adjoining the South Fork of the Republican River. Similar remnant loess prairies have been characterized in western Kansas and Nebraska (Hulett et al. 1968). Considerable debate developed concerning the "pristine condition" of Bonny Prairie, since little bluestem may invade some short-grass prairie sites after cultivation. The land survey notes for the area in the mid–1870s preceded settlement of the area. Survey notes revealed that "grama grass" was common in the vicinity of Bonny Prairie, but that "bunch grasses" dominated the upper slopes above the river valley. The vegetation present on Bonny Prairie is assumed to represent a remnant mixed-grass prairie rather than an artifact from early cultivation.

The Comanche Lesser Prairie Chicken Natural Area is managed by the U.S. Forest Service as part of the National Grassland System. The site, which occurs in extreme southeastern Colorado, has the largest active lek concentration for the state-endangered Lesser Prairie Chicken (*Tympanuchus pallidictincus*). The natural area was greatly modified during the drought of the 1930s and was overgrazed in the past. Sand sage (*Artemsia filifolia*) provides important cover for prairie chickens in the natural area. Blue grama (*Bouteloua gracilis*) and sand dropseed (*Sporobolus cryptandrus*) dominate the understory. No tall-grass species such as sand bluestem (*Andropogon hallii*) are present, although the site appears suitable and these species occur to the west and south of Comanche National Grassland. The land survey notes were reviewed to compare vegetation currently on site with pre-dust bowl conditions. Livestock grazing had already influenced the area by the 1879 survey: "This township is a rolling sandy plain devoid of water but making good enough range for New Mexico stock watering on the Cimarron [River]." Buffalo grass (assumed to be *Bouteloua gracilis*), sand grass (assumed to be *Sporobolus cryptandrus*), and bunch grasses are described from Comanche National Grassland near the study area. No equivalent for bunchgrass currently exists on the site. Surveyors did not mention shrubs in the grassland, although sand sage is presently the dominant cover. The general township description offers little insight:

> the surface of this township consists of rolling prairie, sloping to the southeast, excepting the extreme southern part, which is somewhat broken and hilly. The drainage is southeast through broad, shallow ravines which run in a southeasterly course to the Cimarron River.

Additional historic records will be needed to develop a concept of the vegetation before the dust bowl.

SUMMARY

The General Land Office survey notes are a systematic record providing landscape descriptions for each township and information along section lines concerning tree species, landforms, and streams and wetlands. Surveyor bias, fraudulent descriptions, timing of surveys, and species identifications may limit the use of field notes for reconstructing natural vegetation. However, survey notes are an important historic reference for site-specific studies and when used in conjunction with other historic records, such as photographs, diaries, and journals, provide a valuable image for focusing restoration efforts. Land survey notes are useful in characterizing the landscape at settlement in a number of riparian and grassland areas in the western U.S.

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NEW DISTRIBUTION RECORDS OF SPIDER WASPS (HYMENOPTERA, POMPILIDAE) FROM THE ROCKY MOUNTAIN STATES

Howard E. Evans[1]

Published distribution records of Pompilidae suggest that the Rocky Mountain states (Colorado, Wyoming, Montana) have an attenuated fauna of spider wasps. For the most part, this is a result of the fact that until recently there had been little systematic collecting in these states. In this report, distribution records are presented for 25 species and subspecies not previously reported from these states.

The following list includes records not reported by Townes (1957) or Evans (1950, 1951) and not reported or implied in the Catalog of Hymenoptera north of Mexico (Krombein et al. 1979). Arrangement follows the catalog. Specimens are in the collections of Colorado State University, Fort Collins (CSU), or the University of Colorado, Boulder (UC), except as otherwise noted.

Cryptocheilus hesperus (Banks). CO: 1 ♀, Otero Co., Higbee, 14 June 1966 (pit trap, J. Brookhart) [UC]; WY: 1 ♀, Fremont Co., 3 mi E Moneta, 7 July 1963 (B. Vogel) [UC]. Not previously reported east of Utah.

Priocnemis minorata Banks. CO: 1 ♀, Larimer Co., 13 mi W Livermore, 12 June 1987 (H. E. Evans) [CSU]. Previously reported from forests east of the 100th meridian.

Priocnemis kevini Wasbauer. CO: 2 ♂♂, Larimer Co., 13 mi W Livermore, July, Sept 1983, 1987 (malaise trap, H. E. Evans) [CSU]. Described from Idaho, with a paratype from Michigan, by Wasbauer (1986); identification confirmed by Wasbauer.

Priocnemis scitula relicta Banks. CO: 1 ♀, 1 ♂, Larimer Co., on alfalfa, 9 Aug 1985 (F. Peairs) [CSU]; 1 ♂, Larimer Co., Fort Collins, 4 July 1982 (W. J. Pulawski) [Calif. Acad. Sci.]. Not previously reported west of Wisconsin.

Calicurgus hyalinatus excoctus Townes. CO: 1 ♀, Larimer Co., 13 mi W Livermore, 23 July 1985 (H. E. Evans) [CSU]; 3 ♀♀, Larimer Co., Hewlett Gulch, Aug–Sept 1978 (H. E. Evans) [CSU]. Previously recorded only from New Mexico and Arizona.

Dipogon lignicolus Evans. CO: 5 ♀♀, 2 ♂♂, Larimer Co., 13 mi W Livermore, April 1986, 1989 (reared from trap nests containing fragments of prey, salticid spiders, probably *Phidippus* species; H. E. Evans) [Mus. Comp. Zool., CSU]. Described by Evans, 1987.

Dipogon sericeus Banks. CO: 4 ♀♀, 1 ♂, Larimer Co., Hewlett Gulch, Aug, Sept 1987 (malaise trap, H. E. Evans) [CSU]. Previously reported only from Oregon and California.

Dipogon iracundus Townes. CO: 1 ♀, Boulder Co., Nederland, 25 Aug 1961 (U. N. Lanham) [UC]. Previously recorded only from Arizona.

Auplopus mellipes variitarsatus (Dalla Torre). CO: 2 ♀♀, Larimer Co., Fort Collins, 20 June 1986, 15 July 1987 (black light trap, W. Cranshaw) [CSU]. Widely distributed in northeastern states.

Ageniella rufescens (Banks). CO: 1 ♀, Boulder Co., Hygiene (J. Polhemus) [UC]; 1 ♀, Larimer Co., 20 mi N Fort Collins, 30 Aug 1974 (H. E. Evans) [CSU]. WY: 2 ♀♀, Platte Co., Glendo, 22 Aug 1957 (D. R. Tyndall) [Univ. Wyoming]. Previously reported from Kansas, Texas, New Mexico, and Arizona.

Aporus luxus (Banks). CO: 6 ♂♂, Montezuma Co., Arriola, Sept 1975 (malaise trap, T. Marquardt) [CSU]. A West Coast species; also reported from Utah and New Mexico.

Psorthaspis nigriceps (Banks). CO: 1 ♀, Montrose Co., Uravan, 28 Aug 1947 (H. G. Rodeck) [UC]. Previously known only from

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New Mexico, Arizona, and Utah.

Evagetes c. crassicornis (Shuckard). CO: 1 ♀, Larimer Co., Fort Collins, 21 May 1982 (H. E. Evans) [CSU]; 1 ♀, Larimer Co., 13 mi W Livermore, 20 July 1989 (H. E. Evans) [CSU]. WY: 1 ♀, Platte Co., Wheatland, 24 Aug 1974 [Univ. Wyoming]. A Canadian Zone subspecies. *E. crassicornis consimilis* (Banks) is widely distributed in Colorado and Wyoming.

Sericopompilus neotropicalis (Cameron). CO: 1 ♀, Otero Co., Hawley, 8 Aug 1978 (H. E. Evans) [CSU]. Occurs in Kansas but otherwise not previously reported north of Texas and Arizona.

Episyron quinquenotatus hurdi Evans. CO: 1 ♀, 25 ♂♂, Alamosa Co., San Luis Lake, 19 Aug 1981 (H. E. Evans) [CSU]; 2 ♀♀, Mesa Co., Fruita, 21 May 1963 (B. Vogel) [UC]. Not previously reported east of Utah.

Tachypompilus u. unicolor (Banks). CO: 1 ♂, Larimer Co., 20 mi N Fort Collins, 14 July 1975 (H. E. Evans) [CSU]. I have also seen 1 ♀ from Badlands National Monument, SD, 24 July 1953 (F. Rindge) [Amer. Mus. Nat. Hist.]. Previously reported from the West Coast states east to Utah, Wyoming, and Idaho.

Tachypompilus unicolor cerinus Evans. CO: 1 ♀, 1 ♂, Bent Co., Hasty, 1 July 1982 (W. J. Pulawski) [Calif. Acad. Sci.]; 3 ♀♀, 3 ♂♂, Bent Co., 23 mi S Las Animas, 10 Aug 1986 (H. E. Evans) [CSU]. Previously reported from Utah, New Mexico, and Texas.

Anoplius lepidus atramentarius (Dahlbom). CO: 1 ♂, Baca Co., Two Buttes Reservoir, 9 July 1986 (H. E. Evans) [CSU]; 1 ♀, Larimer Co., 13 mi W Livermore, 27 July 1989 (H. E. Evans) [CSU]. Occurs primarily east of the 100th meridian but extending westward.

Anoplius acapulcoensis (Cameron). CO: 2 ♀♀, 5 ♂♂, Prowers Co., 10 mi W Lamar, 19 July 1974 (H. E. Evans) [CSU]; 1 ♀, 3 ♂♂, Bent Co., Hasty, 26 June 1974 (H. E. Evans) [CSU]; 2 ♂♂, Cheyenne Co., Aroya, 25 June 1974 (H. E. Evans) [CSU]. These represent the northernmost records for this species, which ranges widely in Mexico.

Anoplius percitus Evans. CO: 1 ♀, Douglas Co., Castle Rock, 12 Aug 1962 (S. M. Sutton) [UC]; 1 ♀, Boulder Co., 4 mi NE Lyons, 15 Sept 1962 (U. N. Lanham) [UC]; 1 ♀, 1 ♂, Larimer Co., 13 mi W Livermore, July, Aug 1986, 1989 (H. E. Evans); 4 ♀♀, 6 ♂♂, Larimer Co., Fort Collins and vicinity, June–Aug 1974, 1977, 1985 [CSU]; 1 ♀, Eagle Co., Dotsero, 21 June 1977 (H. E. Evans) [CSU]. An eastern species not previously reported from Colorado. Evans (1970) reported it from Teton Co., Wyoming.

Pompilus silvivagus Evans. MT: 1 ♀, Carbon Co., 5 mi NE Belfry, 24 Aug 1965 (M. Vogel) [UC]. Considerably north of the known range for this species.

Minagenia congrua (Cresson). CO: 3 ♂♂, Larimer Co., Fort Collins, July 1978, 1989 (H. E. Evans) [CSU]. Not previously recorded west of Michigan.

Minagenia montisdorsa Dreisbach. CO: 12 ♂♂, Bent Co., Hasty, 17 July 1974 (malaise trap, H. E. Evans) [CSU]. Previously reported west of the 100th meridian from Texas, Arizona, and Mexico.

Ceropales elegans aquilonia Townes. CO: 1 ♂, Larimer Co., 14 mi N Fort Collins, 7 July 1974 (H. E. Evans) [CSU]; 3 ♂♂, Weld Co., 12 mi NE Nunn, July 1982, 1987 (H. E. Evans) [CSU]. Previously recorded from Minnesota and Alberta. *C. e. elegans* Cresson is more widespread in Colorado.

Ceropales r. robinsonii Cresson. CO: 3 ♀♀, 1 ♂ Larimer Co., 13 mi W Livermore, 7–28 July 1985, 1989 (H. E. Evans) [CSU]. Not previously recorded west of Illinois, although *C. robinsonii stigmatica* Banks is known from Kansas.

In summary, range extensions for spider wasps in the U.S. are verified for the following areas: eight species from the East, eight from the Southwest, five from the Pacific Coast, and three from the North. The remaining species is presently known only from Colorado.

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BATS IN SPOTTED OWL PELLETS IN SOUTHERN ARIZONA

Russell B. Duncan[1,2] and Ronnie Sidner[1]

Analyses of regurgitated owl pellets containing undigested hair and bones permit comparison of species of small mammals not commonly found in pellets with those that are. Results suggest interspecific differences in predator avoidance (Kotler 1985). In addition, new locality records have been obtained, and estimates of population density have been possible (e.g., *Notiosorex crawfordi* [Armstrong and Jones 1972]; bat species in the tropics [Allen 1939]).

Because of the absence or low frequency of occurrence in pellets, bats have been considered an uncommon food for most North American owls (Gillette and Kimbrough 1970, Johnsgard 1988, Long and Kerfoot 1963, Marti 1974). Bats have been listed most frequently as prey of Common Barn Owls, *Tyto alba* (Allen 1939, Kunz 1974, Ruprecht 1979).

Previously, bats have been considered a rare prey item of Spotted Owls, *Strix occidentalis* (Marshall 1942, Wagner et al. 1982). In Oregon, for example, bats comprised only 1% of 4,527 prey items (Forsman et al. 1984). In California, Barrows (1987) identified <1% bats in a sample of 1,829 prey items, and in Arizona, only 2% of 1,193 prey items contained bats (Ganey 1988). Here we report the results of additional analyses of Spotted Owl pellets from Arizona.

Sixty-five pellets and additional fragments were collected from a mated pair of Mexican Spotted Owls (*S. o. lucida*) between 1 January and 23 March 1989 in the Huachuca Mountains, Cochise Co., Arizona (Fig. 1). Pellets were obtained beneath roosts in a steep canyon (elev. 1,737–2,134 m) within montane riparian woodland bordered by mixed-conifer forest and Madrean evergreen woodland (Brown 1982). Dead conifer trees in various stages of decomposition were present. Limestone bedrock was frequently exposed, forming broken cliffs >50m high. Small caves and solution pockets were common, and permanent seeps contributed to a perennial water supply. Pellets were cleaned in 2% aqueous solution of sodium hydroxide to permit identification of skeletal contents (Longland 1985).

Unpublished data were obtained from E. D. Forsman (personal communication), who collected 409 prey items in summer 1977 from pellets of 2 pairs of Spotted Owls in the Chiricahua Mountains (Fig. 1). For comparison, J. L. Ganey's (1988 and personal communication) data are included here on bat specimens among 1,193 prey items collected from 29 pairs of Spotted Owls throughout Arizona during 1984–1987.

Pellets that we collected contained skeletal remains of 39 white-footed mice (*Peromyscus* spp.), 34 woodrats (*Neotoma* spp.), 1 cottontail (*Sylvilagus* sp.), 3 Northern Pygmy Owls (*Glaucidium gnoma*), 1 White-throated Swift (*Aeronautes saxatalis*), 1 unknown bird, 1 mountain spiny lizard (*Sceloporus jarrovi*), and 11 bats (Table 1). Bats comprised 12% of the total prey items.

Thirty-five bats, 8.6% of prey items, were identified in Forsman's (personal communication) sample from the Chiricahua Mountains (Table 1). Ganey (1988) listed 24 bats from Spotted Owl pellets (11 from pellets in southeastern Arizona, Table 1) representing 8% of prey items in southern Arizona but only 2% of total prey items of these owls statewide. The presence of three species of molossids, *Tadarida brasiliensis*, *T. macrotis*, and *Eumops perotis* (Table 1), in pellets provides new records for two of the mountain ranges (see Hoffmeister 1986).

A band and skeletal remains of one *Eptesicus fuscus* (a juvenile male banded by R.

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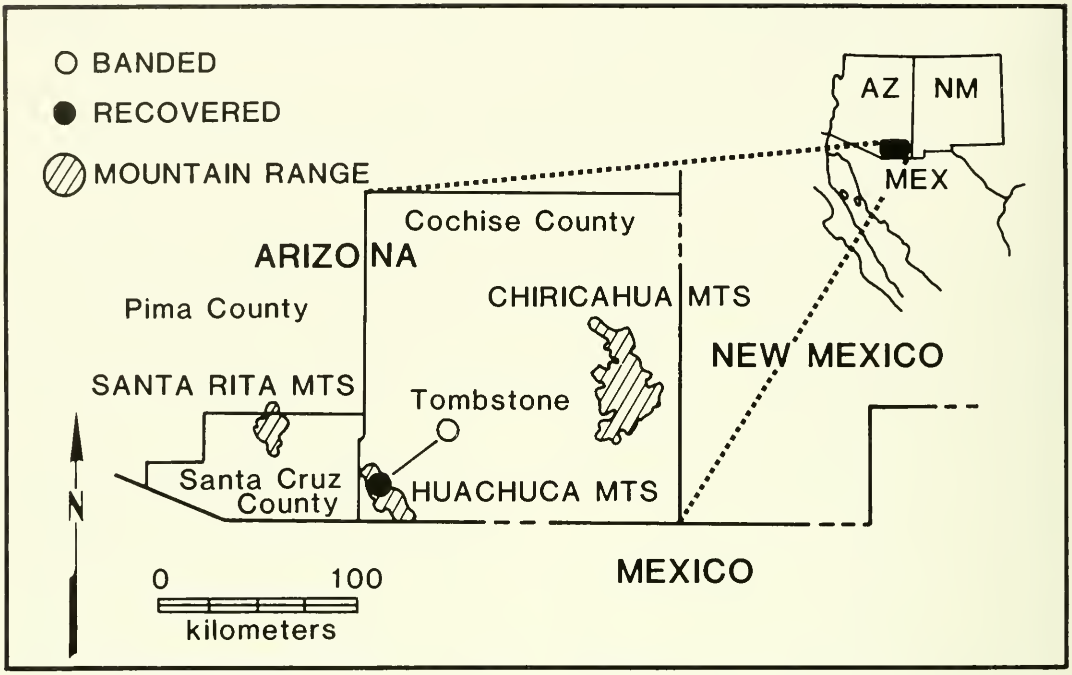

Fig. 1. Huachuca Mountains and surrounding area. Mountain ranges depict relative area above 1,525 m. Locations of banding and recovery sites in Cochise Co., Arizona, are shown for a big brown bat found in a spotted owl pellet.

Sidner and R. Davis on 10 July 1988 at a maternity roost near Tombstone, Arizona) were found in a sample of pellets (dated 7–24 February 1989) from the Huachuca Mountains (Fig. 1). The specimen was found 44 km southwest of the banding site (occupied by bats from May to September only) and is the only off-site recovery of 1,535 banded *E. fuscus.* Because mean home range of mated pairs of Mexican Spotted Owls in northern Arizona is only 847 ha (Ganey and Balda 1989b), recovery of this bat in a Spotted Owl pellet provides information about natural mortality and winter dispersal of *E. fuscus*. It may also suggest the presence of a hibernaculum in the Huachuca Mountains where none is known for this species (Hoffmeister 1986).

Ruprecht (1979) proposed that a high percentage of bat remains occurs among prey items when owl territories overlap home ranges of bats. Pellet analyses have shown that barn owls roosting in the same building with *E. fuscus* consumed a high percentage of these bats (Kunz 1974), while Long-eared Owls (*Asio otus*) roosting in an isolated patch of trees among sand dunes caught only one bat (*Antrozous pallidus*) and 1,365 rodents (Kotler 1985, personal communication). The highest percentage of bats as prey of Spotted Owls was found in our winter sample and reflects the abundance of bat species presumed to have winter ranges in southeastern Arizona (Hoffmeister 1986).

In this study, bats contributed little to total prey biomass of Spotted Owls and simply may have been taken opportunistically. The three species of bats, *E. fuscus*, *A. pallidus*, and *T. brasiliensis*, that were the most numerous in pellets are relatively abundant, colonial species.

Spotted Owls normally employ a sit-and-wait (perch-and-pounce) hunting strategy (Forsman et al. 1984) and are thus unlikely to pursue bats in flight. Mexican Spotted Owls roost and forage in forest adjacent to steep-sided canyons (Ganey and Balda 1989a, 1989b), which provide cool, shaded roosts in trees, cliff ledges, and caves (also used by bats). Owls may take active bats entering or exiting roosts or torpid bats from the interior of roosts (Beer 1953). All bats found in Spotted Owl pellets thus far are species that become

TABLE 1. Bat species from spotted owl pellets in southeastern Arizona. Species are listed for mountain ranges from which the contributors collected pellets. New species records for a mountain range are indicated by *. Numbers in parentheses are individual bats recorded.

Species	Mountain range		
	Chiricahuas	Santa Ritas	Huachucas
Myotis spp.	Forsman (3)		
Myotis californicus (California myotis)			this study (1)
Myotis ciliolabrum (western small-footed myotis)	Ganey (1)		
Lasionycteris noctivagans (silver-haired bat)	Forsman (1)		
Lasiurus cinereus (hoary bat)		Ganey (1)	Ganey (1), this study (1)
Pipistrellus hesperus (western pipistrelle)	Ganey (1)		
Eptesicus fuscus (big brown bat)	Forsman (8), Ganey (2)		Ganey (1), this study (7)
Antrozous pallidus (pallid bat)	Forsman (9), Ganey (1)		
Tadarida spp.	Forsman (1)		
Tadarida brasiliensis (Brazilian free-tailed bat)	Forsman (3), Ganey (2)		*this study (2)
Tadarida femorosacca (pocketed free-tailed bat)	*Forsman (2)		
Tadarida macrotis (big free-tailed bat)	Forsman (4)		
Eumops perotis (western mastiff bat)	*Ganey (1)		
Unidentified bat	Forsman (4)		

torpid during roosting. Bats of this type may benefit beyond energy conservation by selecting darker or less accessible roost sites (Erkert 1982). By comparison, bats that remain alert may stay in the outer, lighted portions of roosts without excessive risk. Two species of bats, Sanborn's long-nosed bat (*Leptonycteris sanborni*) and the Mexican long-tongued bat (*Choeronycteris mexicana*), occur in the three mountain ranges where pellets were collected but do not use torpor or hibernation. Each species hangs alert, making use of lighted portions of roosts (Hoffmeister 1986) and has not been reported from owl pellets collected during any season in Arizona.

Our findings demonstrate that in Arizona, Mexican Spotted Owls utilize a wide vertebrate prey base, suggesting opportunistic foraging as occurs in the northern subspecies (Forsman et al. 1984). Diets may contain a considerable diversity of bats (Table 1), which may be an important component of the winter diet of individual Mexican Spotted Owls in southeastern Arizona.

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SPROUTING AND SEEDLING ESTABLISHMENT IN PLAINS SILVER SAGEBRUSH (*ARTEMISIA CANA* PURSH. SSP. *CANA*)

C. L. Wambolt[1], T. P. Walton[1], and R. S. White[2]

ABSTRACT.—The importance and nature of vegetative reproduction was compared with seedling establishment in plains silver sagebrush (*Artemisia cana* Pursh. ssp. *cana*). Sixty-three percent of plants excavated originated from rhizomes. Sites that experienced habitat disturbance did not have a significantly different number of plants originating from vegetative reproduction than did undisturbed sites. Parent rhizomes were significantly older than taproots, which were significantly older than aboveground stems. Rhizome systems were spread 3.3 times that of plant height. Seventy-nine percent of rhizomatous daughter plants were 100 cm or less from parent plants. Up to 52 sprouts were found on one rhizome. Seedling establishment was greatest during wet growing seasons, and vegetative reproduction was greatest during dry years.

Sagebrush (*Artemisia* L.) taxa are among the most important plants on rangelands of the western United States (Beetle 1977). Plains silver sagebrush (*Artemisia cana* Pursh. ssp. *cana*) is a major consideration in the management of rangelands in the northern Great Plains. This is due to the taxon's competitive nature with livestock forages and its importance as a habitat component for several wildlife species. Together with the other two subspecies of silver sagebrush, mountain silver sagebrush (*A. cana* ssp. *viscidula* [Osterhout]) and Bolander silver sagebrush (*A. cana* ssp. *bolanderi* [Gray] Ward), this complex is encountered on millions of hectares in 13 western states and 2 Canadian provinces (Harvey 1981).

The literature (Young and Evans 1972, Bostock and Benton 1979, Went 1979) provides contradictory evidence as to whether seed or vegetative reproduction is more important for survival of plants displaying both habits in arid and semiarid environments. Accordingly, this will have to be determined for each taxon individually. The most pernicious weeds generally grow from underground roots, rhizomes, and buds (Cook 1983); thus, these are important traits to understand in successful rangeland taxa. Paradoxically, vegetative reproduction in sagebrush taxa has not been previously studied in detail despite the importance of these taxa (Beetle 1977, McArthur and Plummer 1978) and their obvious reproductive success (Harvey 1981). Understanding sagebrush reproductive success would provide insight into plant population dynamics throughout western North America (Mott 1979). Our objective was to assess the importance and nature of vegetative reproduction (sprouting) versus seedling establishment in plains silver sagebrush.

STUDY SITES DESCRIPTION

Six study sites were selected in drainages of the Tongue and Yellowstone rivers near Miles City in southeastern Montana. The sites were considered typical in climatic and edaphic relationships of plains silver sagebrush habitats in the northern Great Plains (Harvey 1981). Soils at each study site are texturally heterogeneous but are largely a mosaic of loams, with silty clay loams predominant. Three sites (Yellowstone River—frigid Ustic Torrifluvents, Lower Black Springs—mixed [calcareous] frigid Ustic Torrifluvents, and Lower Flood—fine montmorillonitic Borollic Camborthids) had experienced fire or ice scraping and shearing in the preceding five years. No evidence of such disturbance was found at the remaining study locations (Lignite Creek—Camborthid Torrifluvents, Paddy Faye—fine montmorillonitic Borollic Camborthids, and Moon Creek—fine montmorillonitic Borollic Natriargids). All sites have received periodic cattle grazing. The area has an average annual precipitation of 340 mm, with peak precipitation received in May and June.

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Methods

Transect Excavations

At each study site a plains silver sagebrush plant 16 to 40 cm in height was located at each 5-m interval along 25-m transects (4). Established plants of this size were selected because rhizomatous connections to parent plants, if present, were still readily apparent. The 20 plants located at each site were excavated to determine whether they had sexual or asexual origins.

Roots were carefully excavated by hand so that fragile rhizome connections remained intact to determine if plants were of independent origin or connected to another plant. Rhizomes were generally found in the top 10 cm of soil, while taproots were excavated to a depth of 1 m or an impenetrable layer. Plants without connecting rhizomes were considered to have originated from seed. Plant height, length of rhizomes, and stem and rhizome diameters were measured on all originally located plants and those plants to which they were directly connected. Root distribution from each excavation was mapped within a grid, and line sketches of each plant were drawn. Samples for age determination (Ferguson 1964) were taken from stem, root, rhizome, and connecting rhizome sections of each excavated plant. Aging of sagebrush was feasible despite the difficulty created by common stem splitting and layering (Ferguson 1964).

To determine whether differences existed in the number of sprouts to seedlings over the six study sites, we conducted a paired Student's t test ($P < .025$). A chi-square analysis ($P < .05$) was performed to learn if fire or ice action on three of the sites was significant in determining the ratio of sprouts to seedlings compared with three undisturbed sites. Analysis of variance (ANOVA) was used for comparison of age and growth means among plant parts. Duncan's multiple range test protected by a prior F-test was used for comparing treatment means.

Isolated Plant Excavations

Two large, well-established plants at the Lower Flood site were the subject of a complete root excavation. Plants were subjectively selected based upon two criteria: (1) the plant had to be relatively isolated from other large plains silver sagebrush plants to minimize major competitive influences, and (2) there had to be an abundance of small plains silver sagebrush plants surrounding the potential parent plant. The two plants selected for excavation were slightly more than 1 m in height. A 5-m area around each of the large plants was excavated so that all roots, including rhizomes of all smaller plants, were exposed. The size of each plant and the root distribution from the excavations were mapped to differentiate seedlings and sprouts. Although we did not analyze the data statistically, our direct observation of the root networks facilitated interpretation of the transect data.

Results

Transect Excavations

Plants arising from rhizomes were more abundant than those that grew from seedlings ($P < .025$) (Table 1). Approximately 63% of the excavated plants were connected by rhizomes to an established plant or rhizome system. Counts of annual rings established that the rhizomatous connections were one to four years old. Usually, a large, established parent plant was the source of rhizomes connecting either single plants or a series of sprouts

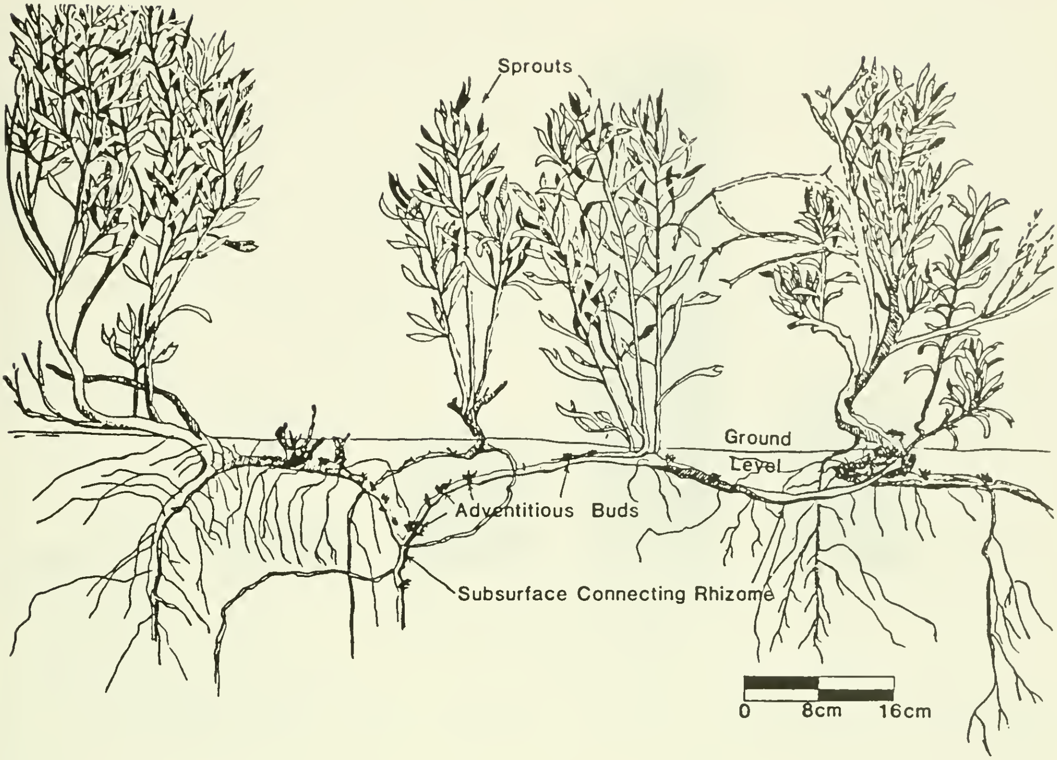

Fig. 1. Graphic example of an excavated sprout connected to a parent plant and other offspring. Original or oldest material is on far right.

TABLE 1. A comparison of the number of rhizomatous to nonrhizomatous plains silver sagebrush plants found at each study site.

	Study site[1]						
	1	2	3	4	5	6	Total
Rhizomatous[2]	13	13	15	7	13	14	75[a3]
Nonrhizomatous	7	7	5	13	7	6	45[b]

[1] Sites are numbered as follows. 1—Yellowstone River, 2—Lower Black Springs, 3—Lower Flood, 4—Lignite Creek, 5—Paddy Faye, 6—Moon Creek.

[2] Plants with rhizome connections (alive or dead) to other plants.

[3] Significant ($P < .025$) differences between rhizomatous and nonrhizomatous plant totals by Student's *t* test are followed by different letters.

(Fig. 1). However, some plants were from a series of sprouts along a rhizome presently terminated with a dead or decadent stump. One site, Lignite Creek, was different in that it had a majority of nonconnected individuals (Table 1). Reduction of available soil moisture due to clay pan soils overlying extensive gravel at Lignite Creek might explain the difference. Plant water use would be less favorable with this condition at the surface, affording an advantage to taprooting plants in reaching deeper, more favorable conditions. The three sites disturbed by fire or ice action were compared with the three undisturbed sites to learn whether the ratio of sprouts to seedlings changed with disturbance. No significant differences ($P < .05$) in numbers of plants arising from rhizomes due to disturbance were found.

Generally, an elaborate subsurface rhizome system was found that was older than aboveground stems. There were significant ($P < .05$) age differences among plant stems, taproots, and parent rhizomes (Table 2) over all six study sites. Aboveground stems were three to five years younger than taproots and associated rhizomes. Parent rhizomes with directly connected sprouts were significantly older than taproots. Taproots and rhizomes without direct connections to a parent plant were not significantly different in age from each other.

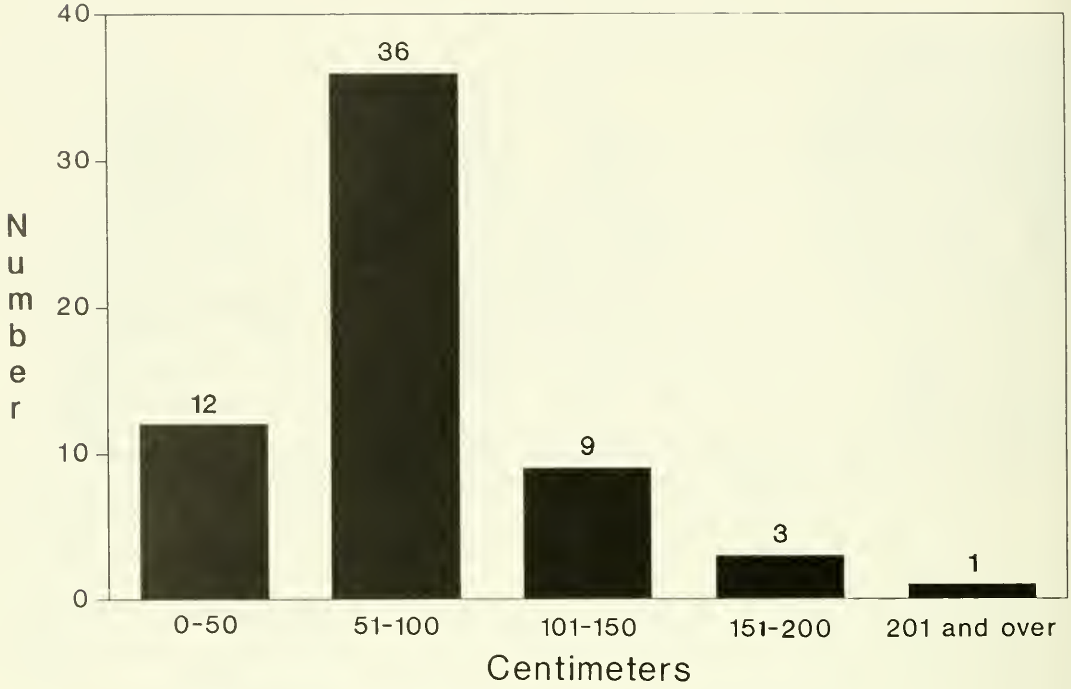

Fig. 2. Number of distances encountered between parents and traceable sprouts of rhizomatous plains silver sagebrush over six study sites.

Table 2. Age relationships of above- and belowground parts of plains silver sagebrush plants from the six study sites.

Plant part	Mean age (years)	Standard deviation	Number of samples
Stems	3.4^{a}[1]	2.0	204
Taproots	6.9^{b}	3.1	28
Parent rhizome[2]	8.8^{c}	3.7	68
Rhizome system[3]	6.0^{b}	2.5	128

[1] Significant ($P < .05$) mean differences by Duncan's multiple range test are followed by different letters.
[2] Rhizome originating from a parent plant (or dead stump) to which sprout was directly connected.
[3] Rhizome sections other than in 2 above.

Table 3. Growth relationships of above- and belowground parts of rhizomatous plains silver sagebrush plants from the six study areas.

Plant part	Mean (cm)	Range (cm)	Number of samples
Plant (sprout) height	32^{a}[1]	11-59	155
Lateral distance to parent connection[2]	78^{b}	14-277	61
Lateral spread of rhizome system[3]	105^{c}	11-369	90

[1] Significant ($P < .05$) mean differences by Duncan's multiple range test are followed by different letters.
[2] Lateral distance from parent plant or rhizome to nearest sprout on rhizome system expressed as a mean of all plants with this growth habit.
[3] Total lateral extent of all rhizomes in an excavation expressed as a mean of all plants with rhizome systems.

Rhizome extension was greater than aboveground heights ($P < .05$) (Table 3), even in older plants that had the largest aerial portions. Rhizome length from the selected plant to the parent plant averaged 2.4 times that of plant height. Total lateral spread of the rhizome system averaged 3.3 times that of plant height.

Figure 2 summarizes the number of distances encountered between parent plants and traceable sprouts. The largest proportion (59%) of these connections were from 50 to 100 cm in length, followed by the 0–50-cm distance (20%).

Isolated Plant Excavations

The extensive sprouting nature of plains silver sagebrush was apparent after excavations had been completed in areas surrounding two large, isolated plants. Most roots were part of a shallow, complex underground network of interconnected rhizomes that often included several smaller, nearly independent

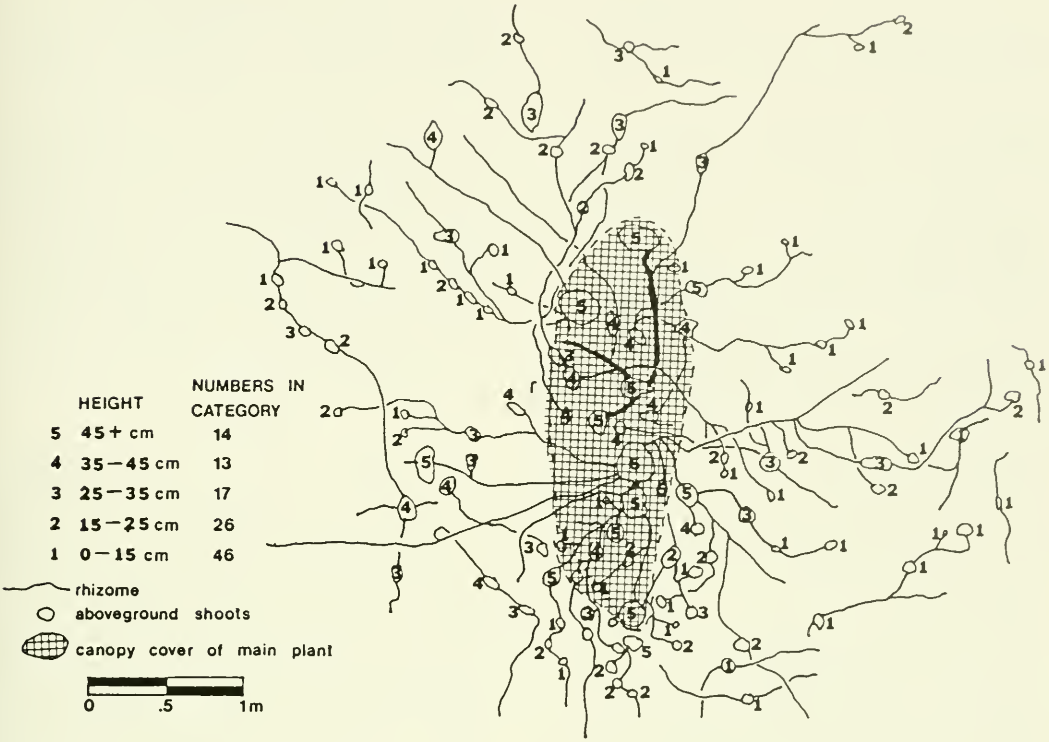

Fig. 3. Diagram of an isolated plant excavation. All aboveground shoots are shown individually and numbered according to height.

systems (Fig. 3). This was most apparent with older, well-established plants from which the network originated (Fig. 3).

Characteristic of the horizontal rhizome expansion were size classes decreasing in concentric circles away from the parent plant. There was considerable variation in rhizome complexity within these individual systems. Excavations established that rhizomes can sprout at least 3 m from the parent plant. Therefore, a large number of progeny may arise asexually from one individual. Individual rhizomes had from 1 to 52 sprouts. No evidence indicated that all individual systems were of the same origin. That is, no common root connections could be traced. However, some might have been connected and later separated after mortality of connective rhizomes.

DISCUSSION

Vegetative reproduction is prevalent in plains silver sagebrush, and the causal agents are of interest and importance to rangeland management. Benefits of vegetative reproduction include (1) an enhanced ability to utilize unevenly distributed resources and (2) an increased competitive ability to occupy adjacent areas (Harper 1977, Cook 1983). In addition, sprouts are better able to resist invasions of seedlings from other species while reducing the probability of extinction. This is accomplished by spreading the risk among many genetically identical individuals (Cook 1983). An evolutionary strategy that employs asexual mechanisms is consistent with the findings of Abrahamson (1980), who reported that increased environmental severity generally shifted emphasis to vegetative reproduction.

Generally, vegetative reproduction is most important where fire, weather phenomena, and other disturbances are common (Bostock and Benton 1979, Went 1979, Abrahamson 1980, Legere and Payette 1981). The sprouting nature of plains silver sagebrush is likely an adaptation to its northern Great Plains habitat. Flooding with associated deposition, along with ice scraping during winter events, is common. Plant production and subsequently fuel loads for fires are relatively high in bottomlands inhabited by the taxon. Consequently, fires are common in plains silver sagebrush habitats. It is logical that plains silver sagebrush is a vigorous sprouter in response to the evolutionary influences of recurring disturbances. This taxon is reported to produce only 18% as many achenes as big sagebrush (*Artemisia tridentata* Nutt.) (Harvey 1981, Tisdale and Hironaka 1981), which likely reflects a reliance on asexual reproduction.

Abundant herbaceous vegetation in mesic flood plains produces substantial competition for seedlings. Vegetative sprouts may compensate through more rapid morphological development. Because sprouts have the advantage of a nutrient reserve from established plants, the sprouting strategy increases survival (Abrahamson 1980).

Although not rare in the communities studied, seedling establishment was found in only one-third of the plants excavated (Table 1). This may be attributable to the inconsistency of specific environmental conditions required for germination and seedling establishment. Environmental factors, especially drought, might best explain differences in ratios of sprouts and seedlings found in 1983. For example, a three-year drought at the study area occurred between 1979 and 1981 when the mean annual precipitation was 23.0 cm and preceded the wet year of 1982 with 41.6 cm of precipitation. The long-term average precipitation is 34.8 cm. This drought coincided with the ages of most plants examined in this study. The relatively moist years preceding (1978 with 44.7 cm) and following (1982 with 41.6 cm) this drought provided the periods of establishment for seedlings at the study sites. However, just as seedlings appear favored during wet years, sprouts were found to have the advantage in establishing during relatively dry periods. The cool, wet growing season of 1982 was followed by a warm, dry (22.3 cm) growing season in 1983. Subsequently, numerous seedlings and few sprouts were produced during 1982, and few seedlings with an abundance of sprouts were produced in 1983. Few seedlings from 1982 survived beyond the dry second season. Therefore, it appears that both the mode and the success of plains silver sagebrush reproduction is strongly related to available moisture as indicated by Salisbury (1942) for wild garlic (*Allium carinatum* L.). Perhaps this influence of climate on reproduction might mask differences of sprout-to-seedling ratios expected between disturbed and undisturbed sites. In our study, these ratios did not vary significantly (Table 1). The reproductive strategies of plains silver sagebrush partially explain the taxon's success and require consideration in managing its habitats for optimum balance between livestock forage production and suitable wildlife habitat.

CONCLUSIONS

We conclude that vegetative reproduction in plains silver sagebrush is the primary means of plant establishment. Although sprouting in this taxon has likely evolved with habitat disturbances, this study did not establish that a greater percentage of plants arising from sprouts should be expected on disturbed than on undisturbed sites. However, annual precipitation does appear to be related to the relative success in initiation and survival of seedlings and sprouts. Seedlings apparently require more moisture for both germination and survival than do sprouts.

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BIBLIOGRAPHY OF NEVADA AND UTAH VEGETATION DESCRIPTION[1]

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ABSTRACT.—Listed in alphabetical order by author are 934 references to literature of the native vegetation of Nevada and Utah. This updates and expands the 1967 bibliography of Christensen for Utah. A keyword-citation index is provided.

This bibliography includes 934 published and unpublished references to studies of Nevada and Utah's native vegetation, 1851–1989. Vegetation is broadly defined as the aggregate of self-reproducing plant species found in an area, or plant communities. This work updates and expands Christensen's (1967a, 1967b) bibliography of the vegetation of Utah. Papers cited in Christensen (1967a, 1967b) that did not refer directly to the study of the vegetation are not included here.

The emphasis is on plant communities, their description, species composition, physiognomy, and ecology, and the techniques and concepts used to recognize and analyze the communities. Our definition of vegetation ecology includes spatial and temporal relations of plant communities to the environment, broadly defined to include soil and climate, and to each other, at all levels, from the biomes to small-scale patterns occurring on a given site. We omitted references dealing solely with the flora of an area. Floras alone do not provide information on the assemblages of species and their relationships to the environment and to each other.

The following subjects are covered exhaustively: classification, community analysis (including structure and function), disturbance, diversity pattern, fire, gradient analysis, grazing, habitat studies, inventory, soil-vegetation analysis, succession, and zonation. Selected references to autecology, population biology, competition, phenology, management, and species range are included only when they specifically address some aspect of the Nevada-Utah vegetation patterns. Coverage of these tangential topics is not comprehensive. The only nonfield studies included are those explaining Nevada-Utah's vegetation patterns. Studies had to be conducted at least in part in Nevada and/or Utah. Many references pertinent to Nevada and/or Utah, but which were completely done in adjacent states, are excluded. Readers are referred to the relevant bibliographies for these citations.

The bibliography lists authors alphabetically. Each reference has been assigned one or more of 28 keywords. First, when applicable, it includes a definition of a broad vegetation type (alpine, desert, forest, grassland, riparian, shrubland, wetland, woodland) using the Unesco (Mueller-Dombois and Ellenberg 1974) definition. The use of riparian is restricted to communities along streams, the use of wetland to communities along all other water formations (lakes, bogs, etc.) The use of these broad terms does not substitute for a formal classification of the study vegetation. They are solely provided for easy retrieval of the appropriate source of information.

The choice of the other keywords (age-size structure, autecology, baseline study, bibliography, classification, community analysis, disturbance, diversity patterns, early exploration, fire, gradient analysis, grazing, habitat type, inventory, map, model, relict vegetation, soil-vegetation relationship, succession, zonation) reflects our own interests in vegetation patterns and not necessarily the author's original emphasis. The total number of keywords was kept small for easy use of the keyword-citation index. Finally, the keywords are used consistently for the same object of study throughout the bibliography.

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CONSERVATION STATUS OF THREATENED FISHES IN WARNER BASIN, OREGON

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ABSTRACT.—Two federally listed fishes, the Foskett speckled dace and Warner sucker, are endemic to Warner Basin in south central Oregon. The Foskett speckled dace is native only to a single spring in Coleman Valley. A nearby spring was stocked with dace in 1979 and 1980, and now provides a second population. The present numbers of dace probably are at their highest levels since settlement of the region. The Warner sucker historically occurred throughout much of the Warner Valley, but its distribution and abundance have been reduced by construction of reservoirs and irrigation dams and the introduction of predatory game fishes. Lentic habitats have become dominated by introduced fishes, particularly white crappie, black crappie, and brown bullhead. The largest remaining population of Warner suckers occurs in Hart Lake, where successful reproduction was documented but there is no evidence of recruitment to the adult population.

Two threatened fishes inhabit separate valleys in Warner Basin, Oregon. In Coleman Valley the only native fish is the Foskett speckled dace, *Rhinichthys osculus* ssp., which occurs in Foskett Spring along the west margin of the Coleman Lake bed. The lake is dry except during years of exceptional rainfall. The dace was listed as threatened because of small population size, trampling of its restricted habitat by cattle, and subsequent degradation of the springpool area (U.S. Fish and Wildlife Service 1985a).

To provide a refuge population free of the effects of intense livestock grazing, 50 dace from Foskett Spring were transplanted on 14 November 1979 into an unnamed spring (now known as "Dace Spring") on Bureau of Land Management (BLM) land approximately 1.5 km south of Foskett Spring. Another 50 dace were transferred into the spring on 26 August 1980. A reproducing population subsequently established in Dace Spring, and more than 300 dace of three size classes were observed there in 1986 (BLM Lakeview District, unpublished data).

The presumed historical range of the Warner sucker, *Catostomus warnerensis*, consisted of the main Warner lakes (Pelican, Crump, and Hart) and other accessible lakes and sloughs in Warner Valley, and low- to moderate-gradient reaches of tributary streams. The species description by Snyder (1908) was based on specimens collected from Deep (= Warner) Creek near Adel. The Warner sucker was listed as threatened primarily because of fragmentation of stream habitats by irrigation diversion dams and the establishment of large populations of introduced piscivorous fishes in lentic habitats (U.S. Fish and Wildlife Service 1985b).

Long-time residents recalled that during the 1930s large numbers of spawning Warner suckers (referred to as "redhorse") ascended Honey Creek far into upstream canyon areas (Andreasen 1975). By the 1970s the species range was fragmented by numerous irrigation diversion dams on the lower reaches of streams tributary to Pelican, Crump, and Hart lakes (Andreasen 1975, Kobetich 1977, Swensen 1978, Coombs et al. 1979, Hayes 1980), which block spawning runs from the lakes into streams.

Coombs et al. (1979) found that although habitats had been fragmented resident stream populations still persisted. Nearly two-thirds of all adult suckers (198 of 300) were captured by Coombs et al. (1979) in the canal between Anderson and Hart lakes, immediately north of the Hart Lake spillway. Adult and larval suckers also were captured in Snyder Creek, in Honey Creek above the dam at Plush, at the mouth of Honey Creek in Hart Lake, at the south end of Warner Valley in Twentymile Creek between the south end of the valley floor and the confluence with Twelvemile Creek, and in Twelvemile Creek immediately above and below the O'Keefe Diversion Dam.

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In 1980 Coombs and Bond (1980) sampled 22 sites throughout the basin, capturing 46 Warner suckers at 4 localities: Honey Creek between Hart Lake and the dam at Plush, canals of Deep Creek at the east end of Pelican Lake, the spillway immediately north of Hart Lake, and Swamp Lake. In 1983 Smith et al. (1984) captured 1 adult Warner sucker in Crump Lake and 2 juveniles (approximately 130 mm total length [TL]) in Deep Creek between Adel and the falls. In 1987 an adult Warner sucker was caught by an angler along the slough just south of Flagstaff Lake (J. E. Williams, personal observation).

This paper summarizes the current status of these two threatened fishes, as determined by surveys conducted from 1987 to 1989. Other native fishes of Warner Valley include a local form of redband trout (*Oncorhynchus mykiss* ssp.), tui chub (*Gila bicolor*), and the common form of speckled dace (*R. osculus*). The Warner Valley redband trout largely has been displaced by introduced trout and is listed as "of special concern" by the American Fisheries Society (Williams et al. 1989).

HABITAT DESCRIPTION AND SURVEY METHODS

The Warner Basin comprises 6858 sq km in south central Oregon and small portions of northeastern California and northwestern Nevada (Fig. 1). Drainage is internal and is divided between Coleman Valley and the much larger Warner Valley. Coleman Valley is a separate drainage in the southeastern part of the basin and receives sparse runoff. Observations of the Foskett speckled dace and its habitat in Coleman Valley were made from 1987 to 1989. Standardized transects were established along Foskett Spring and its outflow to monitor vegetation recovery following cessation of grazing, and to quantify amounts of open-water habitat.

In Warner Valley all water flows into a series of north-south oriented shallow lakes, sloughs, and potholes. During periods with above-average precipitation, as occurred during the early 1980s and again in 1989, these lakes fill from the south and eventually overflow into the northern part of the valley. Only the three most southerly lakes, Pelican, Crump, and Hart, are permanent. Fish collections in Warner Valley were made from 1987 to 1989. Samples were collected from lakes by use of traps, gill nets, and seines, and from streams with dip nets, trap nets, electroshocker, kick nets, and seines. Most fishes were identified, measured, and returned to their habitat. Voucher specimens or those accidentally killed during collecting are housed at the Wildlife and Fisheries Museum, University of California, Davis. Opercles from five suckers were aged according to the methods described by Scoppettone (1988). Visual observations were made of spawning Warner suckers in Honey Creek.

FOSKETT SPECKLED DACE

In 1987 the BLM acquired Foskett Spring and the surrounding 65 ha, of which approximately 28 ha were fenced to exclude cattle. The dace population at Foskett Spring has since expanded to the spring pool, its outflow, and downstream marsh. Baseline water quality and vegetation monitoring at Foskett and Dace springs were initiated by BLM in 1987. The following data collected on 28 September 1988 from Foskett Spring and Dace Spring, respectively, exemplify the two habitat similarities: air temperature 19 and 17 C, water temperature 17 and 16 C, dissolved oxygen 5.3 and 5.9 mg/l, conductivity 350 and 250 mohs/cm, pH 8.1 and 8.2, alkalinity 114 and 99 mg/l $CaCO_3$, hardness 40.0 and 24.7 mg/l, and turbidity 1.4 and 1.8 NTU.

The dace population maintains itself at Dace Spring despite a tendency for vegetation to choke out most open water. The introduced population has expanded by movement of fish through a connecting pipe into a livestock watering trough just east of the spring. No other fish occur in Coleman Valley.

WARNER SUCKER

Surveys on Twentymile Creek above and below the Dyke Diversion Dam located 1 adult and 2 larval Warner suckers in 1988. Additional 1987 and 1988 surveys failed to locate Warner suckers elsewhere in Twelvemile Creek (including sections in Nevada and Oregon upstream of the Nevada border), the canal north of Hart Lake, the slough between Flagstaff Lake and Mugwump Lake, the slough between Lower Campbell and Campbell lakes, or Stone Corral Lake. In April 1989, 28 adult suckers were captured at the

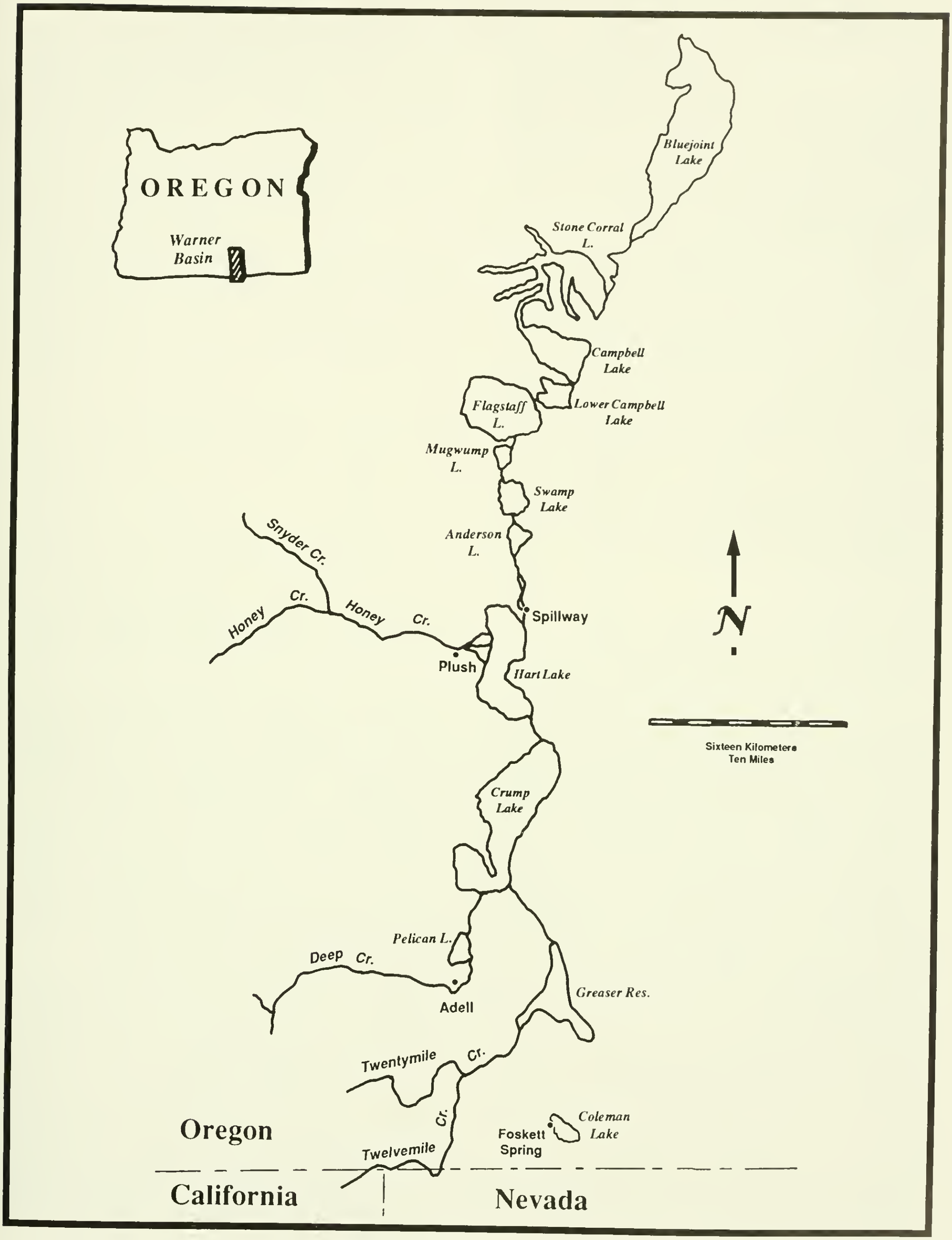
OREGON
Warner Basin
Bluejoint Lake
Stone Corral L.
Campbell Lake
Lower Campbell Lake
Flagstaff L.
Mugwump L.
Swamp Lake
Anderson L.
Snyder Cr.
Honey Cr.
Honey Cr.
Spillway
Plush
Hart Lake
N
Sixteen Kilometers
Ten Miles
Crump Lake
Pelican L.
Deep Cr.
Adell
Greaser Res.
Twentymile Cr.
Cr.
Twelvemile
Coleman Lake
Foskett Spring
Oregon
California
Nevada

Fig. 1. The Warner Basin of south central Oregon.

TABLE 1. Frequency of fishes collected in Warner Basin during 1987–89. All collection sites are in Lake County, Oregon, unless otherwise noted. Collections made at the same habitat are combined.

Location	Warner sucker	Tui chub	Speckled dace	Trout[a]	White crappie	Black crappie	Large-mouth bass	Spotted bass	Brown bullhead
Twelvemile Cr. (Washoe Co., NV)			404						
Twelvemile Cr.			591	51					
Dyke Diversion Canal			1						
Irrigation canal along Twentymile Cr.		1						1	1
Twentymile Cr.	6	25	854	5		2			4
Greaser Reservoir		476				1			2
Deep Creek			400	40					
Hart Lake	70	12			1620	14	1		449
lower Honey Creek	69								
upper Honey Creek			19						
canal north of Hart Lake	7	2			31	30	1		
Anderson Lake		7			10				1
Flagstaff Lake slough		27			107	59			40
slough between Lower Campbell and Campbell		82			39				
Campbell Lake					371				95
Stone Corral Lake		17			5				
Total caught	152	649	2269	96	2183	106	2	1	607
Relative catch (%)	2.5	10.7	37.4	1.6	26.0	1.7	<0.1	<0.1	10.0

[a] May include native redband trout and/or introduced rainbow trout.

mouth of Honey Creek in Hart Lake, and 42 were captured along the east side of Hart Lake. Fish ranged from 311 to 440 mm TL (avg. 385.2, $n = 70$), with most 350 to 410 mm. Approximately 80–100 other adult Warner suckers were observed in Honey Creek between the most downstream diversion dam and Hart Lake. These fish were in breeding condition and migrating upstream, where they were visible because flow in the creek was reduced by upstream diversions. In mid-May 1989 water began spilling from Hart Lake into the canal toward Anderson Lake. Suckers dispersed into the canal, and 7 spawners were collected there in June. Standard length, TL, and age of 5 of these were 331, 357, 7; 307, 361, 7; 333, 387, 7; 335, 390, 9; and 340, 397, 8. Larval suckers also were collected from Honey Creek just above the downstream-most diversion dam, indicating at least limited spawning upstream.

Overall, Warner suckers constituted only 2.5% of all fishes collected during 1987–89 (Table 1). Nearly all suckers were found in Hart Lake, Honey Creek just upstream of Hart Lake, or the canal immediately north of the lake. Introduced fishes dominated the fauna of Hart Lake and other lakes and sloughs in the valley. White crappie (*Pomoxis annularis*) and brown bullhead (*Ictalurus nebulosus*) outnumbered native fishes in our collections from Hart Lake by slightly more than 25:1. Tui chub, which historically was the most abundant fish in lentic habitats, largely has been replaced by white crappie.

The Warner sucker population appears to be largest in Hart Lake, but no recent recruitment could be documented. Except for a small number of larvae in lower Honey Creek, no suckers smaller than 310 mm TL were found. White crappie were abundant at the mouth of Honey Creek during June and may have preyed on sucker larvae as they drifted into Hart Lake. A single trap net set there in June collected 1530 white crappie and 20 brown bullhead.

DISCUSSION

The Foskett speckled dace appears to be near recovery. No exotic species are present in either spring, and the primary threats have been eliminated. Some vegetation needs to be cleared from the pool at Dace Spring in order to provide sufficient open water. Also, fencing along the boundary of Dace Spring should be extended to the east to include additional habitat. Continued habitat and population monitoring are necessary at both springs because the small habitats are vulnerable to slight disturbances.

The largest remaining population of Warner suckers appears to be in Hart Lake, where spawning fish ascend lower Honey Creek and the canal north of the Hart Lake spillway. Populations also may exist in Crump and Pelican lakes.

Successful recruitment of young into the Hart Lake population is limited by reduced spawning habitat in Honey Creek and large populations of crappie. White crappie were introduced into Hart Lake in 1971, and white plus black (*P. nigromaculatus*) crappie were introduced into Crump Lake during 1972 and 1973 (Oregon Department of Fish and Wildlife, unpublished data). Subsequent collections of the Oregon Department of Fish and Wildlife indicated that white crappie, black crappie, and brown bullhead were common in Crump Lake by 1978 (K. Daily, unpublished data) and presumably in Hart Lake as well. Adult white crappie commonly feed on small fishes (Pflieger 1975); thus, their abundance at the mouth of Honey Creek during the same time that larval suckers were collected from the creek increases the likelihood of predation on young-of-year suckers.

Seven irrigation dams on Honey Creek between the lake and Plush result in limited access by adults to upstream spawning areas. During 1989 only two riffles between Hart Lake and the first diversion dam contained suitable gravel for spawning. Depending on stream flows, water-diversion boards may be placed in the irrigation structures before, during, or after the spawning run. Swenson (1978) reported that during 1978 adult suckers migrated as far as the seventh irrigation dam at Plush before boards were installed and water diverted for irrigation.

A remnant population of Warner suckers may persist in Crump Lake, as indicated by collection in 1989 of young-of-year in Twenty-mile Slough below Greaser Dam. Additional surveys of Crump and Pelican lakes are needed to determine the extent of any remaining sucker populations. If present, however, recruitment may be prevented by populations of crappie.

In conclusion, Warner suckers once were common throughout the basin but gradually declined from about 1900 until the early 1970s as a result of agricultural development and placement of irrigation structures in spawning streams. Despite habitat fragmentation and lack of fish passage, recruitment to lake populations continued until the late 1970s, when large populations of piscivorous fishes became established. Recruitment of Warner suckers continues in stream habitats but appears from our observations to be greatly curtailed since 1979.

Control of introduced fishes in Hart and Crump lakes may be impractical because of habitat size (2928- and 3108-ha area, respectively) and large populations. Recovery of the Warner sucker in Hart Lake therefore at least requires increased spawning sites and rearing habitat.

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HOME RANGE AND ACTIVITY PATTERNS OF BLACK-TAILED JACKRABBITS

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ABSTRACT.—Home range use and activity patterns of black-tailed jackrabbits (*Lepus californicus*) in northern Utah were studied using telemetry. Home range sizes ranged from <1 km^2 to 3 km^2 and did not differ between sexes or among seasons. Jackrabbits were inactive during daylight, became active at dusk, and remained active throughout the night. Animals often traversed their home ranges in a few hours. During the breeding season, males were more active than females. Jackrabbits were most active during well-lit nights, and high winds decreased jackrabbit activity.

The black-tailed jackrabbit occupies a wide geographic area and is an important component of the biota throughout its range. In the Great Basin the jackrabbit is the most abundant large herbivore (Wagner 1981) and serves as an important prey item for many predators. Considering the central role of the jackrabbit in many ecosystems, little research on the species has been reported. Detailed quantitative information regarding activity patterns and home range use is lacking. Home range use varies with the patterns of food, cover, and water distribution (Dunn et al. 1982). I examined patterns of jackrabbit activity and home range use throughout a calendar year in shrub-steppe vegetation in northern Utah.

STUDY AREA

The study was conducted in northern Utah near the Wildcat Hills in Curlew Valley, about 10–35 km north of the Great Salt Lake. Topography and vegetation of the area are described in detail by Gross et al. (1974). Four major vegetation types occur in Curlew Valley: (1) open stands of juniper (*Juniperus osteosperma*) at higher elevations, (2) big sagebrush (*Artemisia tridentata*) in the northern portions of the study area, (3) greasewood (*Sarcobatus vermiculatus*) in more saline soils closer to the Great Salt Lake, and (4) expanses of salt-desert vegetation, primarily shadscale (*Atriplex confertifolia*) and saltbush (*Atriplex falcata*), scattered throughout the study area.

Southern portions of the valley are typically more xeric than northern portions, and precipitation is most abundant during winter and spring. Accumulated snowfall in 1983–1984 was 69 cm at Snowville, Utah, 15 km east of the study area, with snowcover persisting from mid-November through mid-March (National Oceanic and Atmospheric Administration 1984).

METHODS

Black-tailed jackrabbit activity and home range use were monitored via telemetry. Incidental direct observations of jackrabbits also aided in describing activity patterns.

Black-tailed jackrabbits were captured by night-lighting and netting (Griffiths and Evans 1970); they were then equipped with radio-transmitters and released. Periodically during each season additional animals were caught and instrumented to replace those that had died. During winter some jackrabbits were captured in live traps and handled similarly to those captured by netting. Sex was determined from external examination of genitalia, and age class was estimated from body size, color, and relative eye size (L. C. Stoddart, unpublished data).

Transmitter collars were designed to minimize chafing of the jackrabbit's neck (Wywialowski and Knowlton 1983). I assume the transmitters had little discernible effect on jackrabbit behavior (Stoddart 1970, Donoho 1972, Brand et al. 1975, Keith et al. 1984).

Telemetry stations on the Wildcat Hills overlooked areas with instrumented jackrabbits. Each station was equipped with two horizontally stacked 5-element yagi antennas, coupled out of phase with a sum-and-difference hybrid junction. A compass rose mounted on the antenna mast indicated the directional orientation of the antennas. A transmitter placed at a known azimuth from each station was used as a beacon to orient the compass rose to true north.

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Home range use was assessed by repeatedly recording azimuths of animals simultaneously from two tracking stations. Four-hour tracking sessions were distributed throughout the 24-hour day with most occurring between dusk and dawn. Locations were recorded every 20 minutes for a 4-hour period on all animals whose transmitter signals could be detected. For each reading it was noted whether the signal varied in amplitude, suggesting movement of the transmitter antenna, which was interpreted as movement by the animal. The amount of night light was classified into one of three categories (low, medium, or high), depending upon the phase of the moon and cloud cover. Wind intensity during the 4-hour period was classified as low or high by noting the wind conditions at the tracking shelters. Periods of no wind were included in the low category.

Home range use was assessed using program HOME RANGE (Samuel et al. 1985b). This program offers a series of statistical tests to derive the appropriate home range estimator (Samuel and Garton 1985). Within each data set locations outside the home range were identified statistically (Samuel and Garton 1985) and discarded (given a weight of 0) if they appeared to be errors or excursions outside the normal home range area (Burt 1943). "Core areas" were identified (Samuel et al. 1985a). As recommended by Samuel and Garton (1985), only data sets with ≥50 locations were analyzed. Comparisons of the sizes of areas used by subsets of the jackrabbit population were made using a two-way analysis of variance (SAS Institute Inc. 1985).

Because of the model-selection criteria of the program, I used the harmonic mean estimator (Dixon and Chapman 1980) for all area-of-use analyses. Dixon et al. (1981) recommended this technique to analyze lagomorph spatial use because it eliminates many problems associated with other analyses.

Choice of a contour isopleth to represent the home range is somewhat arbitrary (Anderson 1982). I chose the 80% contour for jackrabbits because it appears to reflect observed patterns of land use by these animals. To allow comparisons with other published accounts, I also report the 95% contour interval, although it probably overestimates home range size. No statistical rationale exists for the choice of the 95% level, and its use may result from biologists confusing utilization distributions with alpha levels in statistical tests (White and Garrott 1990).

The relationships of time of day, season, sex, amount of moonlight, and wind intensity to jackrabbit activity were assessed using log-linear analyses (Sokal and Rohlf 1981). Terms included in the resulting models reflect significant relationships within the data. Seasons were defined by Curlew Valley weather patterns. Winter ended with the melting of snow in March. Summer began in late June 1984 with the onset of hot temperatures and ended in early September with the arrival of fall rains.

RESULTS

The daily movements of 16 jackrabbits were monitored from February through April 1984, and those of an additional 44 jackrabbits were monitored from June through November 1984. I determined the sizes of areas used by 30 jackrabbits, with 5 animals having 2 areas each, for a total of 35 areas of use (Table 1). The time periods for which areas were measured ranged from eight days to five months. Home range has been defined as the area used by an animal on a day-to-day basis (Burt 1943). How an animal uses its home range affects how long the animal must be monitored before it traverses its entire home range. Typical home range use by black-tailed jackrabbits involved extended use of an area measuring <1 km^2. Animals often traversed the whole area of activity in less than four hours. By dawn a jackrabbit was usually back near the previous day's resting location. Some animals maintained this pattern of space use for up to three months.

Periodically, jackrabbits changed their areas of use. These changes involved extensions of the areas of use into previously unused areas and abandonment of portions of the previously used areas. New areas were then generally used for extended periods. These shifts in areas of use enlarged overall home ranges to 1.5–3 km^2. No differences in the patterns of shifts in areas of use among different sex and age segments of the population

TABLE 1. Black-tailed jackrabbit home range sizes (km^2) (and standard errors) in Curlew Valley, Utah, 1983–1984.

		Harmonic contour area					
Season	Number of animals	95%	SE	80%	SE	core	SE
Adults							
Winter							
Male	2	2.51	0.77	1.66	0.64	0.96	0.33
Female	6	1.25	0.45	0.83	0.28	0.47	0.15
Spring							
Male	5	1.08	0.25	0.73	0.18	0.43	0.13
Female	4	0.85	0.16	0.55	0.13	0.32	0.06
Summer							
Male	5	2.88	0.72	1.83	0.45	1.07	0.31
Female	4	1.63	0.49	1.05	0.29	0.62	0.16
Fall							
Male	1	2.21	—	1.30	—	0.72	—
Female	2	0.87	0.14	0.52	0.10	0.26	0.06
Juveniles							
Summer-fall							
Male	1	1.13	—	0.73	—	0.43	—
Female	5	1.70	0.35	0.92	0.21	0.57	0.15

Two-way analysis of variance using the 80% contour

	df	SS	*F*	*P*
Season	3	3.10	2.35	.10
Sex	1	2.14	4.85	.04
Season × sex	3	0.56	0.42	.74
Error	21	15.41		

were apparent. Core-areas, as identified by program HOME RANGE, encompassed areas slightly larger than half the size of home ranges (the 80% contour) (Table 1) and tended to be near the center of the home range areas.

Jackrabbits changed home range areas seasonally. Where more than one home range was recorded for an animal, each was analyzed independently (Table 1). Areas traversed during seasonal migrations were not considered part of either home range (Burt 1943). In March, just after the winter's snowcover melted, jackrabbits left wintering areas and moved to new home ranges. In the fall many animals abandoned their summer home range areas and moved to wintering areas (Smith 1987).

Wintering areas were located in stands of tall vegetation, primarily greasewood and sagebrush, although a few juniper stands were also used. Wintering areas encompassed only a small portion of the available habitat as jackrabbits concentrated in groups; areas of low vegetation were not used during winter. With spring shifts in home range areas, jackrabbits reoccupied much of the valley (Smith 1987).

Sizes of areas appeared to change seasonally, with areas of use being smaller in spring and fall than in winter and summer. Patterns of home range use also appeared to be similar throughout the year. Males tended to have slightly larger home ranges than females (Table 1). Too few juvenile jackrabbits were instrumented to adequately determine their pattern of home range use. However, sizes of areas used by juveniles and adults did not differ (Table 1). Only juveniles large enough to wear a radio-transmitter (>3 months of age) were instrumented.

Jackrabbit activity changed daily and seasonally (Fig. 1). Significant differences occurred during the day and among the seasons (α = active, β = time, Γ = season; $\ln f_{(ijk)} = \mu + \alpha_i + \beta_j + \Gamma_k + \alpha\beta_{ij} + \alpha\Gamma_{ik} + \beta\Gamma_{jk} + \alpha\beta\Gamma_{ijk}$; $\alpha\beta_{ij}$: $G = 179.5$, 18 df, $P < .001$; $\alpha\Gamma_{ik}$: $G = 594.3$, 20 df, $P < .001$; $\beta\Gamma_{jk}$: $G = 856.3$, 30 df, $P < .001$; $\alpha\beta\Gamma_{ijk}$: $G = 128.8$, 15 df, $P < .001$). Jackrabbits were least active from 0800–1700 hours during the spring, summer, and fall, when they often rested in shallow depressions under shrubs, big sagebrush and greasewood being the most common. In addition, some jackrabbits used badger (*Taxidea taxus*)

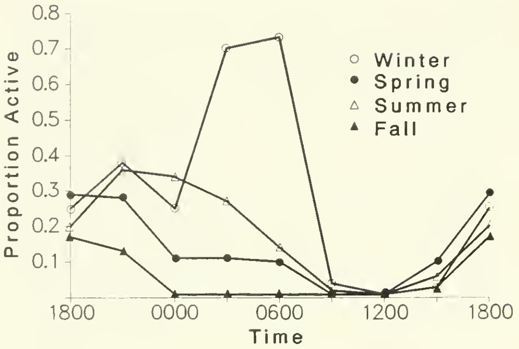

Fig. 1. Frequency of black-tailed jackrabbit activity and relationships with time of day and season of year in Curlew Valley, Utah, 1983–1984.

Table 2. Frequency of black-tailed jackrabbit activity and relationships with sex and season of year in Curlew Valley, Utah, 1983–1984. The data are the number of telemetry readings under the categorical conditions. The proportion active is in parentheses.

		Sex (β)	
Season (Γ)	Active (α)	Female	Male
Winter	yes	129	100
		(.24)	(.29)
	no	409	240
Spring	yes	108	88
		(.16)	(.20)
	no	572	336
Summer	yes	147	156
		(.24)	(.22)
	no	456	555
Fall	yes	21	4
		(.17)	(.04)
	no	101	87

$\ln f_{(ijk)} = \mu + \alpha_i + \beta_j + \Gamma_k + \alpha\beta_{ij} + \alpha\Gamma_{ik} + \beta\Gamma_{jk} + \alpha\beta\Gamma_{ijk}$

$\alpha\beta_{ij}$: $G = 17.6$, 4 df, $P < .005$

$\alpha\Gamma_{ik}$: $G = 94.3$, 6 df, $P < .001$

$\beta\Gamma_{jk}$: $G = 52.3$, 6 df, $P < .001$

$\alpha\beta\Gamma_{ijk}$: $G = 17.0$, 3 df, $P < .001$

burrows during winter, especially when deep snows reduced mobility.

Jackrabbit activity changed seasonally, with jackrabbits least active during fall and most active in winter and summer (Fig. 1). Daily activity patterns also changed seasonally, with jackrabbits less active during morning hours (after midnight) in the fall.

The sexes showed different patterns of activity (Table 2), with males slightly more active than females during winter and spring. Females were slightly more active than males during summer and much more so during fall. The proportion of observations classified as active was lower during fall (Table 2), consistent with the results of the previous analysis (Fig. 1).

Jackrabbit activity was apparently influenced by the amount of light during night hours (Table 3). The proportion of observations in which jackrabbits were active at night changed seasonally, with jackrabbits most active in summer and least active in fall. The relationship of activity and night light also changed seasonally (Table 3). During fall, winter, and spring, jackrabbits were most active when night light was greatest (a full moon and little cloud cover). During summer the amount of night light did not appear to influence jackrabbit activity.

Jackrabbits were most active when there was little wind; high winds were associated with decreased jackrabbit activity (Table 4). Activity in relation to wind intensity changed seasonally (Table 4), with jackrabbits less likely to be active during the winter when winds were high. Sampling of jackrabbit activity during high winds in the fall was insufficient for basing conclusions.

Discussion

Home Range Shape and Size

The shape of most jackrabbit home ranges tended to be elliptical. The shape is not a result of the locations of the tracking shelters in relation to radio-collared jackrabbits, as very acute or obtuse telemetry bearings were excluded from the analysis. A similar elliptical shape was noted by Rusch (1965), who obtained many locations from snow-tracking.

The sizes of black-tailed jackrabbit home ranges determined in this study (Table 1) are larger than those reported for the species in other studies. Rusch (1965) and Nelson and Wagner (1973), also working in Curlew Valley, reported that jackrabbits used areas <0.2 km^2 (minimum convex polygon) for periods of one to two months in the fall and winter. It is not clear why the home ranges I report are greater in size than those described in these earlier studies. Two factors, however, may have had some influence. My relocation effort was more intensive than those conducted previously, resulting in a greater number of relocations per animal. Moreover, advances in

TABLE 3. Frequency of black-tailed jackrabbit activity and relationships with amount of light at night and season of year in Curlew Valley, Utah, 1983–1984. The data are the number of telemetry readings observed under the categorical conditions. The proportion active is in parentheses.

		Amount of light (β)		
Season (Γ)	Active (α)	Low	Medium	High
Winter	yes	133	37	23
		(.21)	(.60)	(.52)
	no	477	25	21
Spring	yes	33	81	48
		(.19)	(.27)	(.42)
	no	138	223	66
Summer	yes	234	77	143
		(.34)	(.31)	(.34)
	no	449	175	273
Fall	yes	12	21	6
		(.09)	(.17)	(.27)
	no	126	104	16

$\ln f_{(ijk)} = \mu + \alpha_i + \beta_j + \Gamma_k + \alpha\beta_{ij} + \alpha\Gamma_{ik} + \beta\Gamma_{jk} + \alpha\beta\Gamma_{ijk}$

$\alpha\beta_{ij}$: $G = 76.0$, 8 df, $P < .001$

$\alpha\Gamma_{ik}$: $G = 103.2$, 9 df, $P < .001$

$\beta\Gamma_{jk}$: $G = 721.5$, 12 df, $P < .001$

$\alpha\beta\Gamma_{ijk}$: $G = 56.1$, 6 df, $P < .001$

TABLE 4. Frequency of black-tailed jackrabbit activity and relationships with wind intensity and season of year in Curlew Valley, Utah, 1983–1984. The data are the number of telemetry readings under the categorical conditions. The proportion active is in parentheses.

		Wind intensity (β)	
Season (Γ)	Active (α)	Low	High
Winter	yes	214	14
		(.32)	(.09)
	no	459	134
Spring	yes	112	52
		(.18)	(.28)
	no	512	211
Summer	yes	392	107
		(.26)	(.21)
	no	1125	396
Fall	yes	33	6
		(.09)	(.27)
	no	318	16

$\ln f_{(ijk)} = \mu + \alpha_i + \beta_j + \Gamma_k + \alpha\beta_{ij} + \alpha\Gamma_{ik} + \beta\Gamma_{jk} + \alpha\beta\Gamma_{ijk}$

$\alpha\beta_{ij}$: $G = 252.3$, 4 df, $P < .001$

$\alpha\Gamma_{ik}$: $G = 704.1$, 6 df, $P < .001$

$\beta\Gamma_{jk}$: $G = 759.7$, 6 df, $P < .001$

$\alpha\beta\Gamma_{ijk}$: $G = 198.8$, 3 df, $P < .001$

radiotelemetric and analytical procedures since the early 1970s may have played an important role.

Lechleitner (1958a) in California, French et al. (1965) in Idaho, and Tiemeier (1965) in Kansas also reported seasonal ranges of <0.2 km^2. Areas of use were determined in these three studies from visual observations of marked animals. Differences in sizes of home ranges may also reflect differences in habitats among study areas. Habitat in Lechleitner's and Tiemeier's studies consisted of pastures and cultivated land. Plant cover on French et al.'s (1965) study area was similar to the native Great Basin shrub-steppe vegetation of Curlew Valley.

Two limitations of the home range analysis may have influenced the results. These are the precision of the tracking system and serial correlation of the location data. I believe that the precision of the tracking system averaged 200 m (Smith 1987, Mills and Knowlton 1989). Sequential locations had to be at least 200 m apart before I could be certain that movement had occurred. Locations closer to the tracking shelters had greater precision, probably to a minimum of 100 m, while locations more distant from the shelters had less precision, probably less than 300 m. The most precise locations were located along the arc created using the baseline between the two towers as the diameter of a circle. The reduced precision in locating distant jackrabbits may have produced overestimates of home range sizes.

Home range estimation methods assume that locations are serially independent (Swihart and Slade 1984). When serially correlated data are analyzed, these methods underestimate home range size. All the location data sets showed some degree of serial correlation. I used all locations obtained for each animal and did not subsample to decrease serial correlation because, for many of the animals, too few locations were obtained to allow me to discard data points and still have a minimum sample size of 50 locations per analysis (Table 1). Because home range size is a statistic, the greatest value of which lies in comparisons among subsets of a population (White and Garrott 1990), I opted for the procedure that gave me larger samples.

Home Range Use

Resting in forms during daylight hours is a behavior observed in virtually all black-tailed jackrabbit populations (Vorhies and Taylor 1933, Lechleitner 1958b, Rusch 1965, Haug 1969, Costa et al. 1976, and Flinders and Elliot 1979). Forms are shallow depressions in or under bushes (Vorhies and Taylor 1933). Form use by Curlew Valley jackrabbits appears typical for the species. The use of burrows during the winter in Curlew Valley, however, appears unusual (Lechleitner 1958b). Jackrabbits use burrows to evade predators (Vorhies and Taylor 1933, personal observation) and construct shallow burrows to escape summer heat in the Mohave Desert (Costa et al. 1976), but daily use of deep burrows has not been reported previously. I believe jackrabbits use burrows during winter in Curlew Valley to reduce the risk of predation (Smith 1987).

Jackrabbits have been reported to use systems of trails to travel about their home ranges (Vorhies and Taylor 1933, French et al. 1965, Rusch 1965). Although trails used by jackrabbits in Curlew Valley were obvious in the snow and vegetation, I was unable to study trail use because the tracking system could not locate jackrabbits with sufficient accuracy.

Home ranges of individual instrumented jackrabbits overlapped extensively. I have no data that suggest individual jackrabbits influenced the home range use by other jackrabbits from spring through fall, although such intraspecific interactions may have occurred. My study suggests that during winter jackrabbits were social and gathered in groups (Smith 1987). Similar winter behavior was reported earlier from Curlew Valley (Rusch 1965) and has also been observed in southern Idaho (personal observation).

Jackrabbits appeared to traverse the entire home range in short periods of time. Similar home range use was reported by Lechleitner (1958a), who observed both female and male jackrabbits covering their ranges in about an hour. French et al. (1965) also reported that jackrabbits traversed home ranges in a matter of hours.

Factors Governing Home Range Shape and Size

Seasonal variation and weather effects.—The greater activity of males compared with females (Table 2) during winter and spring is probably related to reproductive activity. The reproductive season for jackrabbits in Curlew Valley usually begins in January and lasts through May or June (Gross et al. 1974). Black-tailed jackrabbits have a complex mating behavior in which males seek out females (Dunn et al. 1982). Males would thus be expected to be more active than females during the breeding season. Lechleitner (1958a) and Haug (1969) also report greater activity by males during the breeding season.

Other researchers have reported seasonal changes in the daily patterns of jackrabbit activity. Donoho (1972) and Costa et al. (1976) reported that jackrabbits were generally less active during winter. The timing of daily activity observed in this study changed seasonally and was probably related to changes in day length and times of sunset and sunrise. Similar results were reported by Donoho (1972). The evening activity peak I observed is similar to that reported by Lechleitner (1958b) and Haug (1969) (Fig. 1). However, Haug (1969) also described a period of heightened activity just before sunrise.

Blackburn (1968) and Knowlton et al. (1968) reported that jackrabbit activity was influenced by ambient air temperature. I was unable to record air temperatures at jackrabbit locations, but my finding that jackrabbits were less active during high winds tends to support the idea that temperature influences jackrabbit activity. Lechleitner (1958a) and Tiemeier (1965) also reported decreased activity during high winds and inclement weather. Lechleitner (1958a) also noted that jackrabbits were more active during bright moonlit nights, a finding consistent with my results.

The sizes of home ranges measured by this study appeared to change with the seasons, with spring and fall ranges being slightly smaller. Males used larger areas than females. Tiemeier (1965) and Donoho (1972) found no significant differences in home range size between sexes. Other researchers, however, reported that female jackrabbits used larger areas than males in summer, fall (Lechleitner 1958a), and winter (Nelson and Wagner 1973). Differences in procedures, especially analytical, make comparisons among studies difficult. Many jackrabbits changed home range areas on a seasonal basis, with animals moving to wintering areas in the fall and early winter, and leaving in the spring. Rusch (1965), working in Curlew Valley, and Tiemeier (1965), in Kansas, also reported seasonal shifts in home range areas, with animals moving to areas with larger shrubs.

AGE.—As juvenile jackrabbits mature, one would expect their home ranges to increase in size. It appears that juvenile jackrabbits increase the size of their areas of use to roughly that of adults within the first six months postpartum. Young jackrabbits are precocial, are usually weaned by six weeks of age, before the arrival of the next litter, and are independent of their dams at a very young age (Drake 1969).

POPULATION DENSITY.—Jackrabbit populations in Curlew Valley undergo changes in density on a 10-year cycle (L. C. Stoddart and F. F. Knowlton, Mathematical model of coyote-jackrabbit demographic interactions, northern Utah. Poster presented at 4th International Theriological Congress, Edmonton, Alberta, Canada, 1985). My study was conducted during a population low, i.e., < 30 jackrabbits/km^2 (Smith 1987). I do not know whether patterns of jackrabbit home range use change with population density. However, I noted changes in the pattern of use of wintering areas (with fewer wintering areas used during low densities) and habitat types (Smith 1987), suggesting the possibility of other changes in home range use with changing density. Differences between my findings and others reported in the literature may be a function of differing jackrabbit densities.

HABITAT.—Jackrabbit home ranges in this study were contiguous, and separate resting and feeding areas were not used. This reflects the availability of resources within home ranges of Curlew Valley jackrabbits. Where feeding and resting resources are available in the same area, jackrabbits do not need to travel far from daytime forms to nocturnal feeding sites (Vorhies and Taylor 1933, Nelson and Wagner 1973). In areas where feeding resources are separated from cover, jackrabbits have been reported to travel distances >1 km nightly (Vorhies and Taylor 1933, Haug 1969). Jackrabbits have also been reported to shift feeding sites to feed in agricultural fields (Bronson and Tiemeier 1959).

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HUMPBACK CHUB (*GILA CYPHA*) IN THE YAMPA AND GREEN RIVERS, DINOSAUR NATIONAL MONUMENT, WITH OBSERVATIONS ON ROUNDTAIL CHUB (*G. ROBUSTA*) AND OTHER SYMPATRIC FISHES

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ABSTRACT.—We evaluated distribution, habitat use, spawning, and species associations of the endangered humpback chub (*Gila cypha*) in the Yampa and Green rivers, Dinosaur National Monument, from 1986 to 1989. Adult and juvenile humpback chub were captured in high-gradient reaches of Yampa and Whirlpool canyons where they were rare ($n = 133$, <1% of all fish captured). The fish was primarily captured in eddy habitats in association with 7 native and 12 nonnative fish species. Roundtail chub (*G. robusta*) were widely distributed in eddies, pools, runs, and riffles. Humpback chub ($n = 39$) and roundtail chub ($n = 242$) in reproductive condition were sympatric in eddy habitats during the 5–6-week period following highest spring runoff. River temperatures at this time averaged about 20 C. Nonnative channel catfish (*Ictalurus punctatus*) were abundant in eddies yielding humpback and roundtail chubs, suggesting a potential for negative interactions between the native and introduced fishes.

The humpback chub (*Gila cypha*), a large-river cyprinid endemic to the Colorado River basin of western United States, is federally protected by the Endangered Species Act of 1973. The fish persists only in isolated locations, including canyon reaches in the Little Colorado and mainstream Colorado rivers, Arizona (Kaeding and Zimmerman 1983), upper Colorado River, Colorado (Valdez and Clemmer 1982, Kaeding et al. 1990), Green and Yampa rivers, Colorado and Utah (Holden and Stalnaker 1975a, 1975b, Tyus et al. 1982), and mainstream Colorado River, Utah (Valdez 1990). All stocks are presumed native except in Cataract Canyon of the Colorado River, Utah, where some fish may be derived from a 1981 stocking of juvenile fish of upper Colorado River (Black Rocks) parentage (J. Valentine, personal communication).

Distribution and status of humpback chub in the upper Green and lower Yampa rivers in Dinosaur National Monument (DNM) remain poorly documented, partly because canyon-bound whitewater habitats are difficult to access and sample, the fish is rare, and diagnostic features are not well established. Humpback chub were first reported in DNM in the 1960s, and most captures occurred in the confluence area of the Yampa and Green rivers (Holden and Stalnaker 1970, 1975a, 1975b, Vanicek et al. 1970). Studies in the mid–1970s and early 1980s also noted the paucity of the fish in DNM (Seethaler et al. 1979, Miller et al. 1982).

Roundtail chub (*Gila robusta*) are sympatric with humpback chub in DNM but are more widely distributed and more abundant (Banks 1964, Vanicek et al. 1970, Holden and Stalnaker 1975, Miller et al. 1982). The fish is not considered threatened or endangered under the Endangered Species Act of 1973. Remains of *Gila* species in Indian sites in DNM dating more than 1000 years old (Leach 1970) suggest that chub were presumably eaten by Native Americans and thus have been present in the area for a long time.

This study was initiated as part of a larger program to assess status and habitat needs of endangered fishes in the Yampa River (Tyus and Karp 1989). Our objectives were to locate humpback chub in DNM and, if successful, evaluate habitat use (including flow and temperature requirements), identify spawning areas, and determine species associations.

METHODS

The lower 73.6 km of the Yampa River (i.e., Yampa Canyon: Deerlodge Park to Echo Park; Fig. 1) was sampled weekly from mid-May through early July 1987–1989 by electrofishing and angling with native foods (e.g., Mormon crickets [*Anabrus simplex*] and megalopteran larvae) and night crawlers at various locations in the water column. Echo and Island parks and Whirlpool and Split Mountain canyons of the Green River were sampled

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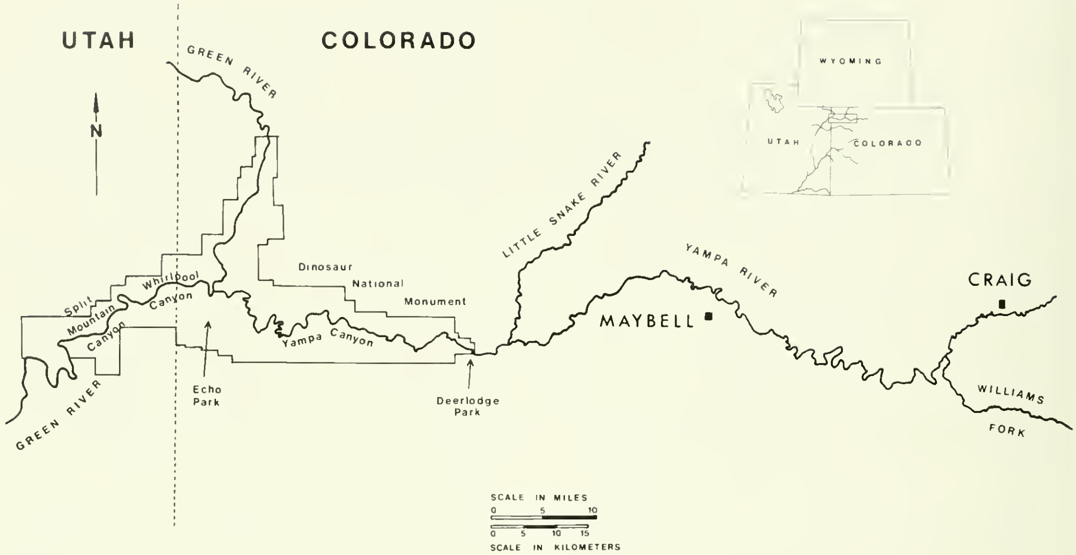

Fig. 1. Yampa and Green rivers, Colorado and Utah, showing the boundaries of the study area and Dinosaur National Monument.

at least twice each spring in 1987 and 1988, and Lodore Canyon (Green River) was sampled once each spring. Survey sampling (including trammel netting) was conducted throughout the Monument in July 1986 to locate humpback chubs. Use of trammel nets was discontinued after this effort because of trauma to the fish.

Sampling trips in Yampa Canyon occurred at weekly intervals (preceding and following first and last capture of ripe fish) to insure an accurate assessment of the humpback chub spawning period. Our efforts were less intensive in the Green River portion of the Monument because earlier sampling had yielded few adult chubs in these reaches (Holden and Crist 1981, Miller et al. 1982). Sampling preceded peak flows and was suspended during highest runoff (2–4 week period depending on water year) because of sampling problems in high water. Sampling ended each summer with attainment of base flows (approximately late June to early July). Our efforts were restricted to the spring and early summer because of boat accessibility. However, two areas in Yampa Canyon that yielded humpback chub in the spring (Big Joe Rapid and vicinity, Warm Springs Rapid and vicinity) were sampled in September 1989 via helicopter and by foot to assess habitat availability, use, and substrate composition during low flows.

All chubs greater than 85 mm total length (TL) were identified to species using established morphological characters (Smith et al. 1979, Douglas et al. 1989). We did not evaluate habitat use of young humpback chub because we could not reliably distinguish young of the various *Gila* species. Humpback chub greater than 250 mm TL were tagged with uniquely numbered Carlin-dangler tags for recapture information (e.g., growth and movement data). Sex determination was based only on expression of eggs or milt from ripe fish, either spontaneously or following manual pressure on the abdomen. Fish with breeding tubercles but without expressible sex products were considered in reproductive condition.

Riffles, small rapids, runs, eddies, pools, and backwaters were sampled. Because water turbidity precluded visual contact with humpback chub, it was necessary to estimate the point of capture. Physical habitat parameters recorded at each humpback chub capture included water depth, temperature, and substrate type. Depth was measured with a calibrated rod, gross substrate type was described from visual and manual examination, and temperatures were obtained with hand-held thermometers (methods after Nielsen and Johnson 1983). We did not attempt quantification of water velocities because most humpback chub were captured in habitats where water currents swirled in both upstream and downstream directions and initial efforts with a flow meter yielded a wide range of positive (upstream) and negative (downstream) velocities. Habitat use data was not recorded for species other than humpback chub. River flows were obtained as daily averages from the U.S. Geological Survey gauging station at Deerlodge Park, Yampa River (Fig. 1). Stream gradient was obtained from U.S. Geological Survey stream profile maps.

Data Analyses

Capture data were analyzed by total catch (all years, all gear types, and sampling) and standardized catch (1987–1989: catch of all species and effort recorded for each sample). Total catch data were used to describe general fish distribution, and standardized data were used to evaluate relative abundance. Standardized catch data were summed by gear (i.e., angling or electrofishing) and for each river reach (i.e., Yampa, Lodore, Whirlpool, and Split Mountain canyons, Echo and Island parks), and catch per unit effort (C/f) was calculated by dividing numbers of fish captured by effort. Angling and electrofishing data from 1986 were not included in C/f estimates because numbers of fishes other than chubs were not recorded and because of significant differences in angler ability. Trammel netting C/f was not reported because of limited use. Electrofishing was biased toward catch of larger individuals, and small fishes (e.g., nonnative reside shiner [*Richardsonius balteatus*] and native mottled sculpin [*Cottus* spp.]) and juveniles of larger species were not recorded because they often slipped through our 1-in^2 mesh dip-nets. Angling efforts in September 1989 were excluded from the C/f estimates because this effort represented a unique fall sample. Sampling was initiated late in 1986, and those data were excluded from our evaluation of spawning period.

RESULTS

Distribution and Habitat Use

HUMPBACK CHUB.—Humpback chub were collected only in whitewater reaches of Yampa (n = 130) and Whirlpool (n = 3) canyons (Fig. 1). The Whirlpool Canyon fish were captured in the same location, about 6 km downstream of the confluence with the Yampa River. No other humpback chub were captured in the Green River. Humpback chub constituted 7.3% (n = 51) of the standardized angling and <1% (n = 58) of the standardized electrofishing catch. They were most abundant (85% of all humpback chub captures, n = 113) in the upper 44.8 km of Yampa Canyon, a moderately steep-gradient section (3.2 m/km) dominated by rocky runs, riffles, and rapids. Lower Yampa Canyon (km 0–28.8), a lower-gradient system (1.0 m/km) consisting mostly of long, deep runs and incised meanders, yielded relatively few humpback chub (n = 17).

During spring runoff, humpback chub were most often captured in larger shoreline eddies (20–100 m^2) that were either downstream of boulders or upstream of rapids, or in smaller eddies (<20 m^2) within shoreline runs. Adult fish (>230 mm TL; based on capture of the smallest ripe fish, a 232-mm-TL male) were consistently captured in, and apparently selected, seasonally flooded shoreline eddies (i.e., formed and maintained by spring runoff). These habitats were dominated by low or negative water velocities and influenced by river surges (i.e., water velocities at any particular point varied in magnitude of up- and downstream currents). Substrate consisted mostly of sand and boulders, and water depth averaged 1.3 m at the estimated point of capture. Humpback chub were not collected in riffles and rapids.

Eleven of 76 Carlin-tagged humpback chub ($\bar{x}$ = 312 mm TL, SD = 19) were recaptured one week to two years after initial capture (5 within a year, 6 from one to two years). Ten fish were recaptured in the immediate vicinity of their original capture, and one was collected about 8 km downstream from its initial capture site. Eight fish (73%, n = 11) were recaptured in breeding condition on at least one occasion. We detected no growth in recaptured fish.

About 22% (n = 29) of humpback chub were juveniles (88–228 mm TL). These were most often captured by electrofishing in rocky shoreline runs and small shoreline eddies. One juvenile (122 mm TL) was taken from the stomach of a 61-cm-TL garter snake (*Thamnophis* species) caught at the confluence of the Yampa and Green rivers.

ROUNDTAIL CHUB.—A total of 1482 roundtail chub were captured in all reaches of DNM except Split Mountain Canyon and the upper 29 km of Lodore Canyon. The fish constituted 37% ($n = 256$) of the standardized angling and 15% ($n = 1016$) of the standardized electrofishing catch. Roundtail chub were at least three times more abundant in Yampa Canyon than in the DNM portion of the Green River (Tables 1, 2) and were most prevalent in the upper 44.8 km of Yampa Canyon (73% of all roundtail chub captures, $n = 1085$). The fish was incidental in Lodore Canyon (<1%, $n = 3$). Adults and juveniles were most often captured in eddies, pools, and shoreline runs, but they were also taken in riffles and lower portions of rapids.

Species Associations of Humpback Chub

Humpback chub were captured in association with 7 native and 12 nonnative fish species (numbers of native sculpins and nonnative redside shiners not recorded). Species that dominated the standardized catch included flannelmouth sucker (*Catostomus latipinnis*), bluehead sucker (*C. discobolus*), roundtail chub, common carp (*Cyprinus carpio*), and channel catfish (*Ictalurus punctatus*) (Tables 1, 2).

A total of 350 fish were captured by angling in eddies occupied by humpback chub. Roundtail chub composed about 45%, channel catfish 35%, and humpback chub 15% of this catch. More channel catfish were captured by angling than was any other species ($n = 328$, 47% of angling catch), and it was the most abundant nonnative fish in eddies that also yielded humpback chub. Other species, including Colorado squawfish (*Ptychocheilus lucius*), flannelmouth sucker, common carp, black bullhead (*Ameiurus melas*), and rainbow trout (*Oncorhynchus mykiss*), composed less than 5% of the angling catch. Electrofishing catch was dominated by flannelmouth ($n = 2049$, 29%) and bluehead ($n = 1801$, 26%) suckers, and these fishes were common in canyon habitats (Table 1) and open parks (Table 2).

The most abundant introduced fishes in DNM were common carp ($n = 1321$) and channel catfish ($n = 1153$). These species were relatively common in canyon-bound whitewater reaches and lower-gradient slowwater sections. Standardized C/f data indicated both were most abundant in Split Mountain Canyon (Tables 1, 2).

During September 1989, flows in Yampa Canyon were reduced to less than 2.83 m^3/s, and fish habitat was limited to shallow riffles (about 15-cm depth) and deeper pools and runs (about 1-m depth). On September 7 we collected five chubs (four roundtail and one suspected roundtail × humpback chub hybrid) and seven channel catfish in pools and eddies (about 1 m deep) in Big Joe Rapid (km 38.4). Other chubs, including a suspected humpback chub, were observed about 0.8 km upstream in a 1.1-m-deep pool created by shoreline boulders. No fish were observed or collected in the vicinity of Warm Springs Rapid (km 6.4) on September 14.

Spawning of Humpback Chub and Roundtail Chub

Thirty-nine humpback chub (16 ripe males, 5 ripe females, and 18 tuberculate but nonripe fish) were captured in shoreline eddy habitats in a 48-km reach (km 20.8–68.8) in Yampa Canyon ($n = 37$) and in a 2-km reach (km 545.6–547.2) in Whirlpool Canyon ($n = 2$). Turbidity precluded direct observation of the fish; thus, spawning behavior and microhabitat use were not documented.

All ripe fish were silvery colored with "gold flecks" on the dorsum. Ripe males always had some orange coloration on the lower side of the head, opercles, abdomen, and paired and anal fin bases. Ripe males and females usually bore light tuberculation on portions of the head, nuchal hump, opercles, and paired fins. This tuberculation was more robust in males. Ripe males averaged 311 mm TL ($n = 16$, $SD = 35$, range 232–370 mm) and 229 g ($n = 14$, $SD = 67$, range 130–348 g), ripe females averaged 300 mm TL ($n = 5$, $SD = 20$, range 280–333 mm) and 230 g ($n = 4$, $SD = 75$, range 160–336 g), and nonripe tuberculate fish averaged 303 mm TL ($n = 18$, $SD = 35$, range 232–382 mm) and 203 g ($n = 17$, $SD = 62$, range 92–356 g).

Ripe humpback chub were collected following highest spring discharges from mid-May to late June 1987 to 1989 (Table 3, Fig. 2). Captures of nonripe but tuberculate fish also occurred within this 5–6 week period (Table 3). Although sampling in 1986 did not include prerunoff conditions and thus was excluded from Figure 2, four humpback chub in

TABLE 1. Total catch (N) and catch per unit of effort of fishes collected by standardized angling (AN) and electrofishing (EL), 1987–1989, Yampa, Lodore, Whirlpool, and Split Mountain canyons, Dinosaur National Monument. Total effort in hours spent angling (angler hours) and electrofishing.

		Yampa Canyon		Lodore Canyon	Whirlpool Canyon		Split Mountain Canyon
Species	N	AN	EL	EL	AN	EL	EL
			Native species				
Flannelmouth sucker	2,159	0.30	28.94	24.72	0.00	27.82	20.92
Bluehead sucker	1,812	0.01	22.35	14.43	0.00	31.96	83.67
Roundtail chub	1,238	3.25	17.09	0.28	1.02	2.66	0.00
Humpback chub	109	0.65	1.03	0.00	0.23	0.00	0.00
Colorado squawfish	27	0.01	0.30	0.28	0.00	0.53	1.02
Razorback sucker	4	0.00	0.07	0.00	0.00	0.00	0.00
Mountain whitefish	2	0.00	0.02	0.00	0.00	0.13	0.00
			Introduced species				
Common carp	1,100	0.24	15.06	10.94	0.23	9.19	25.51
Channel catfish	1,091	4.01	9.64	1.79	2.61	8.26	71.94
Trout[a]	277	0.01	0.16	22.26	0.00	3.86	1.02
Black bullhead	31	0.11	0.21	0.09	0.68	0.4	0.51
Northern pike	15	0.00	0.18	0.00	0.00	0.13	2.04
White sucker	13	0.00	0.14	0.18	0.00	1.73	0.00
Smallmouth bass	6	0.00	0.11	0.00	0.00	0.00	0.00
Green sunfish	1	0.00	0.02	0.00	0.00	0.00	0.00
Total fish	7,885	653	5,349	795	42	641	405
Total effort[b]		76	56	11	9	8	2

[a] Includes rainbow, cutthroat, brown, and lake trouts.
[b] Rounded

TABLE 2. Total catch (N) and catch per unit of effort of fishes collected by standardized electrofishing (EL), 1987–1989, Island and Echo parks, Dinosaur National Monument. Total effort in hours spent electrofishing.

		Island Park	Echo Park
Species	N	EL	EL
Native species			
Flannelmouth sucker	185	26.37	26.34
Bluehead sucker	145	21.54	19.95
Roundtail chub	42	3.22	8.18
Mountain whitefish	1	0.32	0.00
Introduced species			
Common carp	125	19.29	16.62
Channel catfish	55	11.9	4.6
Trout[a]	16	0.64	3.58
Black bullhead	2	0.00	0.51
Northern pike	1	0.00	0.26
White sucker	1	0.32	0.00
Green sunfish	2	0.32	0.26
Total fish	575	261	314
Total effort[b]		3	4

[a] Includes rainbow, cutthroat, brown, and lake trouts.
[b] Rounded

TABLE 3. Capture dates of humpback and roundtail chubs in reproductive condition, Yampa and Green rivers, Dinosaur National Monument, 1986–1989.

	Ripe males	Ripe females	Tuberculate fish[b]
		Humpback chub	
1986[a]	Jul 5–15	Jul 5	—
1987	May 20–Jun 29	May 18–Jun 16	May 18–Jun 22
1988	Jun 7–28	Jun 15	Jun 6–15
1989	Jun 7	—	May 27–Jun 6
		Roundtail chub	
1986[a]	Jul 6–29	—	—
1987	May 18–Jun 20	May 17–Jun 23	May 17–Jun 29
1988	Jun 7–Jul 5	Jun 16	Jun 7–29
1989	May 27–Jun 7	Jun 20	May 22–Jun 20

[a] No sampling prior to July 5 in 1986.
[b] Tuberculate fish were not ripe but exhibited secondary sex characters.

breeding condition (two of each sex) were collected in July of that year. Ripe fish were captured at water temperatures of about 19.5 C (range 14.5–23 C).

Roundtail chub in reproductive condition ($n = 242$: 117 males, 6 females, and 119 tuberculate but nonripe fish) were darker than

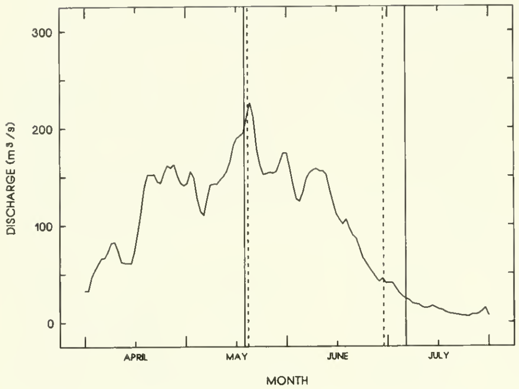

Fig. 2. Relationship between average distribution hydrograph and spawning period for humpback and roundtail chubs, Yampa River, 1987–1989. Dashed vertical lines delineate first and last capture of ripe humpback chub; solid vertical lines delineate first and last capture of ripe roundtail chub; 1986 not included because sampling was initiated late in spring runoff.

humpback chub and exhibited more robust tuberculation and more brilliant orange coloration. Patterns of tubercles and breeding coloration were similar between the two chubs. Ripe male roundtail chub averaged 344 mm TL (*n* = 117, *SD* = 24, range 292–419 mm TL) and 329 g (*n* = 100, *SD* = 84, range 190–652 g), and ripe females averaged 363 mm TL (*n* = 6, *SD* = 15, range 343–380 mm TL) and 363 g (*n* = 3, *SD* = 104, range 276–478 g). Nonripe tuberculate fish averaged 351 mm TL (*n* = 119, *SD* = 29, range 264–447 mm TL) and weighed about 364 g (*n* = 77, *SD* = 123, range 140–844 g).

Ripe roundtail chub were captured in pools and shoreline runs and eddies during the period of declining spring runoff (Fig. 2). Humpback and roundtail chubs in breeding condition were collected syntopically on 13 occasions. Although this indicated overlap in use of shoreline eddies during spring runoff, ripe females of both species were not syntopic.

DISCUSSION

Humpback chub and roundtail chub were sympatric in DNM in the reach from upper Yampa Canyon to upper Whirlpool Canyon, although humpback chub were rare (<1% of total catch and only 8% of the two *Gila* species combined). Humpback chub were most prevalent in, and presumably selected, eddy habitats in moderate- to steep-gradient reaches, whereas roundtail chub were ubiquitous in parks and most canyons in eddies, riffles, and runs. Both fishes were most abundant in Yampa Canyon; neither was captured in Split Mountain Canyon, and the humpback chub was absent and the roundtail chub rare in Lodore Canyon.

The paucity of Colorado River chubs in Split Mountain and Lodore Canyon reaches indicates a general decline of *Gila* species relative to earlier decades (e.g., Banks 1964, Vanicek et al. 1970, Holden and Stalnaker 1975a). This may be related to the loss of historic temperature and flow regimes due to regulated flow releases from Flaming Gorge Dam, and to the proliferation of nonnative fishes, particularly channel catfish and common carp. The current rarity of Colorado River chubs in Split Mountain Canyon was also noted by the authors in 10 hours of opportunistic sampling and by the State of Utah during their 1988–89 studies (T. Chart, Utah Division of Wildlife Resources, personal communication).

Capture of 133 humpback chub, including 39 breeding adults and 29 juveniles, indicates that a reproducing population exists in Yampa Canyon. However, only one ripe fish, a male, was collected in the Green River (i.e., Whirlpool Canyon), and it is unknown whether it spawned there or was a stray from the Yampa River. Collection of ripe roundtail chub in canyon reaches yielding ripe humpback chub indicates some temporal and spatial overlap in habitat use during the spawning period, as observed by others in the upper Colorado River (Kaeding et al. 1990).

Ripe humpback and roundtail chubs were collected during declining spring flows and increasing river temperatures after highest spring runoff. This occurred in May and June in low- (e.g., 1987, 1989) and average- (e.g., 1988) flow years but extended into July in the 1986 high-flow year. No humpback chub in breeding condition were captured during prerunoff and late postrunoff periods, and we presume the fish spawned only during the 5–6 week period following highest spring flows. Capture of only a few ripe female chubs (five humpback and six roundtail chubs, 4% of all breeding captures) suggested that females may be ripe for a limited time. Ripe humpback chub were captured at temperatures ($\bar{x}$ = 19.5, range = 14.5–23 C) that approximate optimum egg incubation conditions (i.e., 20 C; Marsh 1985). These temperatures are similar to the 14–24 C range noted by Kaeding et al. (1990) but slightly higher than the 11.5–16 C temperatures noted by Valdez and Clemmer (1982), both in the upper Colorado River.

All humpback chub and most roundtail chub in breeding condition were captured in shoreline eddies. Our recapture data indicate that adult humpback chub remain in or near specific eddies for extended periods and that they return to the same eddy during the spawning season in different years (i.e., they exhibit a fidelity to a specific site). Ten of the 11 recaptures were captured in the same eddy as the initial capture (50% in two different spawning seasons), and 73% were captured in breeding condition at least once. We do not know whether these fishes deposited eggs in these eddies or used such habitats only for staging, resting, or feeding. However, we consider the use of such habitats as part of the breeding requirements of humpback chub in the Yampa River. Shoreline eddy habitats in Yampa Canyon were ephemeral (i.e., disappeared with declining summer flows), and it was obvious that the fish moved elsewhere after the spawning period. Our observations of *Gila* species in pools near Big Joe Rapid in September 1989 suggest that some fish remain in nearby deep habitats during low-flow periods.

Feeding habits of humpback chub are not well known and were unknown in DNM. Capture of some fish in the interfaces between shoreline eddies and adjacent runs suggests that chubs use these areas for feeding on drift. Stomachs of two humpback chub that died in trammel nets contained hymenopterans and plant debris; and gross examination of fecal material taken from live fish indicates extensive use of hymenopterans and other terrestrial insects (e.g., Mormon crickets) as food. We observed humpback chub and other fishes (e.g., roundtail chub, common carp) feeding on Mormon crickets at the water surface in eddies.

The high numbers of channel catfish in habitats used by humpback chub and roundtail chub and the gross overlap in foods consumed and in feeding habits (Banks 1964, Holden and Stalnaker 1975a, Tyus and Minckley 1988, Tyus and Nikirk 1990) indicate a potential for negative interactions between these fishes. Although the incidence of predation by channel catfish on native fishes is unknown, observations of bitelike abrasions on some chubs collected in DNM suggest channel catfish predation because no other piscivorous fish in that system could have caused such damage. Humpback chub remains were found in channel catfish stomachs from the Little Colorado River (W. L. Minckley, personal communication), and channel catfish are known to consume fish, fish parts, and eggs in DNM (Tyus and Nikirk 1990). Only a few common carp were captured syntopically with humpback chub. However, we speculate that their abundance may also have some negative impact on the native fishes, due perhaps to predation on eggs.

The humpback chub persists in only a few canyons in the Colorado River basin, and planned water development projects may further jeopardize its survival. The Yampa River in DNM supports all native fishes known to have occurred there, including the endangered humpback chub, Colorado squawfish, and razorback sucker (*Xyrauchen texanus*). Existing flows of the Yampa River may be singularly responsible for enabling the persistence of chubs in the Yampa and Green rivers. Alteration of Yampa River flows could reduce the availability or character of chub spawning habitat and presumably adversely affect their reproduction, aid in further proliferation of introduced competitors and predators, and reduce the quality and quantity of usable habitats. Dinosaur National Monument should be considered a refugium for native fishes, and efforts should be made to protect flows of the Yampa River.

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MANAGEMENT OF ENDANGERED SONORAN TOPMINNOW AT BYLAS SPRINGS, ARIZONA: DESCRIPTION, CRITIQUE, AND RECOMMENDATIONS

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ABSTRACT.—Efforts between 1982 and 1990 have failed to recover and secure three natural populations of endangered Sonoran topminnow (*Poeciliopsis o. occidentalis*) at Bylas Springs, Arizona. Flooding in the Gila River in 1977–78 allowed ingress by predatory mosquitofish (*Gambusia affinis*), and topminnows began to decline. Since that time (1) one stock has been replaced twice and is again nearly gone because of depredations by mosquitofish that resisted two eradication attempts; (2) topminnows at a second spring were extirpated through vegetation encroachment after fencing to protect the habitat from livestock; and (3) a third population was lost to mosquitofish, restocked after the nonnative was removed, and the restocked population is again in jeopardy, or extirpated, since mosquitofish reinvaded. Recommendations for a more intensive program of recovery are based on reassessments of past efforts and new suggestions for eradication and exclusion of mosquitofish.

The Sonoran (Gila) topminnow, *Poeciliopsis o. occidentalis*, is a poeciliid fish endemic to and once widespread in the Gila River basin of Arizona and New Mexico, USA, and the ríos Gila, Concepcíon, and Sonora basins of Sonora, México (Hubbs and Miller 1941, Minckley 1973, Vrijenhoek et al. 1985). It was listed in 1967 as an endangered species (U.S. Fish and Wildlife Service [USFWS] 1989) because of predation by introduced mosquitofish (*Gambusia affinis*) and habitat degradation in the Gila River basin (Miller 1961, Meffe et al. 1983, Meffe 1985). Most efforts to recover the Sonoran topminnow have emphasized reintroductions within its native range (USFWS 1984). This paper deals only with attempts to maintain its natural populations, which in the USA are now restricted to fewer than 10 sites, all in Arizona.

STUDY AREA

Three natural topminnow populations occupied a series of small springs adjacent to the Gila River on San Carlos Apache Indian Tribal lands near Bylas, Graham County, Arizona. Two were discovered in 1968 (Johnson and Kobetich 1970) and the third in 1981 (Meffe et al. 1983). No other fishes were present. Although collectively known as Bylas Springs, the habitats gained various coined names in the literature. For brevity, we term them S-I (with west and east sources) through S-III, west to east, and provide a synonymy below. Descriptions and/or mention of the springs have appeared in papers noted above and others by Meffe (1983a, 1983b), Meffe and Marsh (1983), Hendrickson and Minckley (1985), Williams et al. (1985), Taylor (1987), and Hershler and Landye (1988).

All the springs are small, with base flows of a few liters (S-II = Middle Spring, which dried temporarily in 1990) to a few tens of liters per minute (S-I, with west and east sources, = Bos and Medicine springs, respectively; S-III = Salt Creek). S-III has the greatest base flow. S-I and S-II rise through alluvial fill along a stony escarpment; they have essentially no surface watersheds other than their immediate surroundings. S-III rises in the channel of an otherwise ephemeral watershed of >50 km^2 (Burkham 1976a). All are intermittent in their lower reaches, originally isolated from the Gila River either by desiccating on or percolating into the terrace that parallels the river's broad floodplain (S-I and S-II), or by falling over an alluvial escarpment >2.5 m high (S-III).

Unusually high flooding in the Gila River in winter 1977–78 afforded an opportunity for mosquitofish to invade S-I, and that species plus red shiner (*Cyprinella lutrensis*; recorded only once) also colonized S-III. Subsequent declines in topminnow populations

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were immediate and dramatic in both systems, and various management strategies were planned and implemented in attempts to eradicate the introduced fish and restore topminnows. This paper recollects those efforts, provides a status update on topminnows at Bylas Springs, and offers recommendations to perpetuate the stocks.

THE SEQUENCE OF EVENTS

Quantitative data are lacking on the abundance of topminnows at the times of their discovery in Bylas Springs, but these fish were present in substantial numbers, especially in summer throughout the systems and in winter in and near the springheads. After invasion of mosquitofish, topminnow in S-I between summer 1980 and spring 1982 remained in the upper reaches of runs (62–72% of all fishes present) but declined to rare or absent downstream where mosquitofish were numerous. A parallel situation existed in S-III. S-II was never invaded by mosquitofish, and topminnows remained common until 1988.

S-I.—In March 1982 S-I was poisoned with antimycin-A (Meffe 1983b). No live fish were found three weeks later, and >150 topminnows, along with large numbers of indigenous invertebrates salvaged prior to poisoning, were reintroduced in the springheads. By July 1982 substantial populations of both topminnows and invertebrates were reestablished. At the same time, however, mosquitofish were discovered downstream. Since the Gila River had not again flooded, poisoning must have failed to remove them from the lower part of the system. Meffe (1983b) recommended massive, repeated poisoning combined with construction of barriers as a possible method of maintaining the topminnow. Both strategies were embraced in the species' recovery plan (USFWS 1984).

Barriers intended to prevent upstream movements of mosquitofish were constructed on the runs of all three springs during winter 1983–84. Each consisted of low (0.7–0.8 m), concrete, V-notch weirs with earthen wings at S-I and S-III extending laterally and upstream for 3.5–6.6 m. No berms were constructed lateral to the barrier at S-II. In addition, the western source of S-I and the single source of S-II, plus the areas surrounding each new barrier, were fenced to exclude domestic livestock.

S-I was again poisoned with antimycin-A in April and June 1984 and restocked in July with >200 topminnows and uncounted invertebrates removed prior to poisoning. All native animals soon reestablished in large numbers. However, mosquitofish again survived downstream, to reinvade above the barrier when it was bypassed by spate-augmented flows in late summer. The introduced species constituted 24% of total fishes caught in December 1985, 69% in September 1986, and 98% by July 1987 (Simons 1987). In January 1989 topminnows ($n = 9$) in the fenced (west) source of S-I were accompanied by mosquitofish ($n = 6$), and only mosquitofish were taken downstream; the unfenced (east) source was not sampled. Three topminnows and one mosquitofish were collected from the fenced source in April 1990, while topminnows composed 44% of 189 fish taken from the unfenced source. No topminnows were found in the pool above the barrier or in the stream below, where mosquitofish were abundant.

In summer 1989, in anticipation of another poisoning (which has not yet occurred), the channel of S-I was realigned to again flow over its barrier, and low (<0.5 m high) gabions of wire-constrained and loose rock were extended for 19–24 m on either side to replace the earthen berms. In summer 1990 notches in all the barriers were reshaped from the original "V" to approximately rectangular, doubling their areas to 1500 cm^2 to accommodate larger flows. The upstream base of the barrier at S-I was also sealed with bentonite to prevent seepage under the structure, which had become substantial, and a large saltcedar (*Tamarix chinensis*) that threatened damage was removed.

S-II.—This spring experienced no discharge that passed over the barrier and remained secure from mosquitofish; nevertheless, topminnows disappeared in 1990 due to surface water depletion. Invasion by cattail (*Typha angustifolia*) after livestock exclusion, discussed below, resulted in increased evapotranspiration and accumulation of vegetative debris and entrained sediment that dried the system.

S-III.—Topminnows were extirpated from S-III by 1984. A flood in the Salt Creek watershed in 1983 incised the lower part of the run to destroy the former waterfall. The intermittent, lower part of the spring run now led into the river over a gentle cataract that should have posed no reasonable deterrent to fish passage. Despite this, the reach above the artificial barrier remained fishless from the time mosquitofish were poisoned in April 1984 until 300 topminnows from S-II were stocked in 1986 (Brooks 1986). Topminnows became abundant, and no exotic fish was captured in 1986, 1987, or winter 1988. The run flooded around the barrier sometime in 1988, and mosquitofish again appeared in spring-summer 1989. By April 1990 mosquitofish constituted 76% of all fishes collected above the barrier and were abundant downstream where only a single topminnow was captured. No topminnows were observed in S-III in July 1990.

In 1989, in anticipation of future renovation and as at S-I, lateral gabions of wire-constrained and loose rock were extended 10–11 m on either side of the structure, and the channel of S-III was realigned to again pass over its artificial barrier.

DISCUSSION

The inability to secure populations of the endangered Sonoran topminnow at Bylas Springs is disturbing, given that nearly a decade has passed since management efforts began. Moreover, of the 10 known natural stocks of Sonoran topminnows remaining in the Gila River basin (including S-I and S-II, the latter now extirpated), 6 were sympatric with mosquitofish in 1987 (Simons 1987) and expected to disappear in the near future.

There is little doubt that two of the three populations at Bylas Springs would already be gone had mosquitofish not been partially controlled, but the facts remain that (1) a topminnow stock at S-I, although removed and replaced twice, is again nearing extinction through depredations by mosquitofish that resisted two attempts to remove them; (2) a native stock at S-II has been extirpated through encroachment of vegetation after fencing to protect it from livestock; and (3) one population (S-III) was lost to mosquitofish, necessitating restocking from S-II after the nonnative was removed, and the restocked population is again in jeopardy, or extirpated, since mosquitofish reinvaded.

Major habitat changes occurred as a result of barrier construction and fencing in the Bylas Springs system. All the runs begin at a relatively low gradient, which is reduced even further as they pass onto the gently sloping surface of the Gila River floodplain. This precluded construction of high barriers without extensive concrete work or excavation for long, lateral berms. The structures decided upon were placed as far downflow as practicable (ca 400 and 200 m downstream from the respective west and east sources in S-I, 60 m in S-II, and 575 m in S-III) to protect maximum lengths of spring runs. All barriers are 700 m or more from the Gila floodplain. None spanned the entire flood channel, however, and those at S-I and S-III failed to direct high discharges over the concrete weirs, since surface runoff from one or more precipitation events cut around them. Berm replacement by longer rock gabions in 1989 again failed at S-I, where surface flow bypassed the barrier in July 1990.

The barriers also created small ponds on the low-gradient runs. Concern existed that such ponds might enhance mosquitofish, and the exotic species did, in fact, quickly expand its population as soon as the lentic habitat was achieved. However, because they had already invaded prior to the presence of ponds, the question was moot. The pond habitats were transitory anyway. Sedimentation was extensive, and all three were quickly invaded by cattails. By 1990, emergent vegetation was so dense above the barriers on S-I and S-III that open water scarcely existed. Cattail stands had trapped even more sediment, so that bypassing by floodwaters may have been forced in part by mounding of vegetative debris and silt upstream from the weirs. Given sufficient time, accumulations of cattails became so extensive that we are convinced the barriers would have been clogged and breached without high water.

In January 1989 the barrier pool at S-II held only small pockets of water, 20–30 cm in diameter and scarcely a centimeter deep. Several dozen topminnows had died in these pockets, likely due to combined low temperature and oxygen depletion in the thin layer of water overlying organic sediments. The population had dwindled to a few individuals, and a single adult male was caught. In April and July 1990 the habitat was only moist; no fish were found despite exhaustive examination.

A similar sequence occurred after fencing to exclude cattle from the source of S-II. The headspring and its outflow were rapidly invaded by cattails, and by January 1989 the plants had formed a virtual mound of living and dead vegetative materials, with surface water only along the margins. We speculated that the site would be uninhabitable by fishes the next growing season, and by April 1990 no surface water was present and the topminnow population was gone. Succession had proceeded to include invasion of a large bulrush (*Scirpus* sp.). In July 1990 water was present but fishless, and the cattail stands here and at the downstream barrier pool were dead for unknown reasons.

Vegetation in the western source of S-I responded differently to livestock exclusion. The marsh and springhead, although <5.0 m in diameter, were avoided by livestock, presumably due to its dangerously spongy, "quaking," organic deposits overgrown by "cienega" vegetation of small sedges (*Eleocharis* sp.) and grasses. Only its periphery was heavily grazed. Over the years Minckley (unpublished data) found three dead cattle mired in the center of this tiny marsh. It remains similar today inside its protective fence, although there is a slightly more luxuriant growth of the same low vegetation but no invasion of cattails. Invasion by other than low, especially adapted sedges and grasses may be precluded by water-saturated, reducing hydrosoils, as suggested by Hendrickson and Minckley (1985). Interestingly, the spongy marsh has now solidified and no longer appears dangerous to livestock. Currently, the fish habitat comprises only a limnocrene, ca 50 cm long, 25 cm wide, and 25 cm deep, and its outflow.

The eastern source of S-I was always larger than any other spring but Salt Creek, and remains so. It was not fenced and remains an open, flowing limnocrene 1.0 m across, 2.0 m long, and 25 cm deep. The combination of intense watering/grazing/trampling by livestock plus human activities, although unsightly and outwardly appearing to damage the system, precludes overgrowth by semiaquatic vegetation.

Recommendations

Our recommendation is that the U.S. Fish and Wildlife Service make a firm, appropriately funded commitment to maintain the Bylas Springs topminnow stocks. Piecemeal efforts to date have largely failed because hydrologic and vegetational dynamics and complexity were either not understood or taken into account. Habitat responses to management prescriptions were thus unpredicted. A formal plan for recovery must be implemented, followed by programmed, event-responsive monitoring for the foreseeable future.

Next, it is appropriate to define the degree of isolation of the three Bylas Springs. The presence of endemic hydrobiid snails, members of a specialized group restricted to springs in the American West (Taylor 1987, Hershler and Landye 1988), indicates considerable antiquity of the habitat. These animals are essentially unknown in streams, and their presence in large, erosive rivers like the Gila is even less probable. Their presence in S-III, which rises within a channel that floods on occasion, is unusual. Topminnows could have colonized the springs at any time.

Mosquitofish were not locally available to invade Bylas Springs until perhaps the 1930s. Chamberlain (1904) collected none in the Safford area, and the species was found nowhere else in Arizona until 1926, when it appeared in the Colorado River at Yuma and Salt River in Tempe (Miller 1961, Miller and Lowe 1967). Invasion progressed rapidly, and mosquitofish were abundant statewide at low elevations by the 1940s (Minckley 1973). Topminnows were thus protected for about 40 years, until flooding in 1977–78 was sufficient to permit ingress by the nonnative species. Reconstruction of the history of these habitats helps understand how and why mosquitofish were originally excluded.

The Gila River channel, <90 m in width in the period 1875–1903, was eroded to an average of 600 m in width in 1905–17 (Burkham 1972, Turner 1974). The terrace on which Bylas Springs now occur was not present in the latter period, and the springs were much nearer or could have flowed directly into the river.

During 1905–1906 a cone of coarse alluvium was washed into the Gila River channel by flash flooding in Salt Creek (the channel in which S-III rises). By 1914 the river was being deflected southward and threatening the town of Bylas (U.S. Army Corps of Engineers

1914, Olmstead 1919). This was accompanied by deposition on the north side of the channel, downstream of the Salt Creek alluvial cone, as documented by photographic evidence (Burkham 1972) and indirectly by the sizes of mesquite trees (*Prosopis* sp.; see Gavin 1973) that could only have colonized after the terrace was formed (see also Minckley and Clark 1984). In part because of saltcedar invasion (Burkham 1976b), the channel again narrowed, to average <120 m by 1964–68. The river remained on the south side of its floodplain; thus Bylas Springs were isolated. Flooding in 1977–78 and again in 1983 continued to erode southward, stimulating major engineering attempts to stabilize and control the channel (personal observation).

Since it was unknown whether invasion by mosquitofish in 1977–78 was an isolated event or whether the system was changed enough to assure continued access by exotic fishes, we reexamined it in July 1990. S-I ended, as it did before 1977–78, in a variably wetted sump formed within saltcedar thickets on the terrace. This sump may exceed 0.5 ha in area and was heavily utilized by livestock. Also, as before, there was no apparent outlet to the Gila River, which lay at least a kilometer farther south and considerably lower in elevation (ca 5.0 m). S-II similarly remained equally as isolated in 1990 as it was in the recorded past. As noted before, the channel into which S-III rises passed unimpeded into the Gila River and was thus accessible to mosquitofish during flood.

As long as mosquitofish exist in the sump of S-I, an artificial barrier will be required, but it must be designed to function under all but the most severe conditions. S-II seems sufficiently isolated without a barrier, assuming fish habitat can again be established. S-III will require a barrier for the foreseeable future, since mosquitofish will continue to occupy the Gila River. Existing weirs, especially those for S-III, will require further modifications to accommodate high discharges or must be replaced with structures that will do so. The last is difficult because of the gently sloping surrounding terrain, which may necessitate berms extending tens of meters on each side. Each should be equipped with wide spillways of nonerodable material. We also recommend installation of soil pipe or some other means of passing base flows through all barriers so that upstream ponds and their associated problems will not exist.

Once mosquitofish are eradicated, a barrier should not be needed on S-II. Forty years of protection by natural isolation would seem an acceptable period of time for management of an endangered, short-lived species such as the Sonoran topminnow. We cannot predict the recurrence interval of major floods, but such events, some of which have exceeded 4000 $m^3 \cdot sec^{-1}$ in a river that averages 14 $m^3 \cdot sec^{-1}$ at Safford (Burkham 1970, U.S. Geological Survey 1989), cannot be engineered against. Such a flood, directed against the north side of the Gila River floodplain, would destroy the system as it now exists.

Despite these data and pronouncements, mapping of the entire spring complex is clearly in order for future management reference. The effort should include aerial photography at the time of minimum vegetative development in winter, accompanied by extensive ground truth to confirm intricacies of the aquatic system. The extent of aquatic habitat should be determined under both drought and wet conditions to assure an understanding of actual and potential interconnections.

Next, mosquitofish must be eradicated, an operation which must be preceded by removal of substantial numbers of native fish and other animals from each spring to secure refugia. Fortunately, fish from S-II have already been transplanted to a spring in Roper Lake State Park near Safford, Arizona, where they established a large, reproducing population (Arizona Game and Fish Department [AZGFD], unpublished data). A stock from S-I is being similarly maintained at Arizona State University. The stock originally inhabiting S-III is extinct.

Invertebrates may present a problem, especially the two endemic hydrobiid snails, *Tryonia gilae* and the monotypic *Apachecoccus arizonae* (Taylor 1987, see also Hershler and Landye 1988), which have previously been held on-site for no longer than a few days and in aquaria for about three months. If these animals are to be held captive for a longer period, special treatment or facilities may be required. Typically, invertebrates may be reintroduced soon after the poison dissipates, generally a few days after the final application. Numbers of all animals retained for restocking should be large enough to assure maintenance of genetic variability and a reasonable probability for representation of rare alleles (Meffe 1986, 1987, Meffe and Vrijenhoek 1988).

Considering the negative results of previous attempts, piscicide should be applied repeatedly, perhaps three or more times at weekly or longer intervals. Application should be accompanied by physical dewatering of runs, lateral pools, and the downstream sump of S-I, if possible. Footprints of livestock in muds of the sump provide tiny, but effective, life-support sites in which mosquitofish may survive immediately adjacent to toxic water. Temporary exclusion of livestock might well alleviate this problem. Alternatively, water could be retained upstream by temporarily damming the spring run, so the sump could be repeatedly dewatered, at least to a degree, and then flooded to inundate such refugia with poisonous water.

A fishless period of at least a year should be required for the entire system before topminnows are restocked. Presence of mosquitofish in any of the springs allows children (or adults) to inadvertently or intentionally move them from place to place. Humans are attracted to springs in otherwise arid lands, and the Bylas Springs, although reasonably isolated, are periodically used by local residents for recreation.

In order to assure long-term success, the area must be inspected frequently and managed to assure maintenance of habitat integrity and continued exclusion of mosquitofish, and to detect and interdict local land uses that may prove detrimental. We recommend a cooperative agreement with the San Carlos Apache Tribe to perform a quarterly or more frequent schedule of surveillance and monitoring. Biannual, intensive surveys should enlist the assistance of a professional biologist. The entire system is small and may be thoroughly examined in one day.

The activities of domestic livestock, which must have precluded overgrowth by cattail in the past, may be a necessary part of the ecology of these springs. Encroachment by semiaquatic vegetation destroys small, isolated habitats, and this must be avoided. The habitat disruption and apparent degradation by livestock is preferable to loss of the habitats and topminnows. If reliable, close-order surveillance is developed, the existing fences could be gated and opened periodically to allow removal of vegetation by livestock. If not, we recommend the fences be removed from headsprings and barrier pools alike.

Cattail and other emergent plants could also be controlled by cutting, burning, or chemical herbicides; but these methods are labor-intensive and may be more habitat disruptive than livestock, a situation that should be avoided if possible. Experimental manipulations to determine reasonable vegetation control measures might be attempted at S-II, which is now fishless. Once tested, acceptable control techniques could be applied to other sites.

Conclusions

The current and past recovery efforts in behalf of Sonoran topminnows in the Gila River basin (Brooks 1985, 1986, Simons, 1987, Simons et al. 1989) have emphasized introductions and reintroductions within historic range far more than dealing with natural populations, resulting in continuing jeopardy to natural populations. In fact, according to the current recovery plan (USFWS 1984), all natural populations could disappear without influencing the down-listing or delisting criteria. And, since the criteria have been satisfied (Simons et al. 1989), the species could conceivably be down-listed to threatened status. In 1990 the USFWS Desert Fishes Recovery Team recommended against such action (Minckley, unpublished data).

We do not underestimate the difficulties associated with habitat renovation for maintenance of native topminnow stocks, but we suggest a concerted effort be directed toward accomplishing that end at Bylas Springs. If topminnows cannot be secured here, which undoubtedly represents some of the least complex habitats occupied by natural populations of topminnows in the USA, it seems highly unlikely that any natural population threatened by mosquitofish has much hope ofa persisting. Yet, repeated attempts to eradicate mosquitofish have failed, and other efforts to manage the habitat have had undesirable results. It is more efficient to devote necessary planning, manpower, and material to initial operations, even if the assurance of success is costly, than to expend lesser amounts on repeated, unsuccessful operations over time, whereby cumulative costs become exorbitant and the populations are still lost. A new round of effort is clearly needed, and quickly.

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DAM-SITE SELECTION BY BEAVERS IN AN EASTERN OREGON BASIN

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ABSTRACT.—We compared physical and vegetative habitat characteristics at 14 dam sites occupied by beaver (*Castor canadensis*) with those at 41 random unoccupied reaches to identify features important to dam-site selection in the Long Creek basin, Grant County, Oregon. Stream reaches with dams were shallower and had a lower gradient than unoccupied reaches. Beaver did not build dams at sites with a rock substrate. Bank slopes at occupied reaches were not as steep as those at unoccupied reaches; and occupied stream reaches had greater tree canopy cover, especially of thinleaf alder (*Alnus tenuifolia*), than did unused reaches. A discriminant model using transformations of bank slope, stream gradient, and hardwood cover classified all beaver dam sites correctly and 35 of 41 random sites as unoccupied sites. The 6 misclassified sites had rock substrates.

We also tested four habitat suitability models for beaver in this basin. Three models produced significantly different ($P < .05$) scores between occupied and random unoccupied reaches, suggesting that they might have some utility for this region.

Beaver (*Castor canadensis*) have long been recognized as having a significant effect on riparian ecosystems. Through alteration of stream flow, they impact soil moisture, biomass distribution, soil redox potential, pH, and plant-available nitrogen in riparian areas (Naiman et al. 1988). Creation of pool habitat is important to some salmonids (Gard 1961) and other pool-inhabiting animals, particularly in areas lacking pools formed by naturally occurring, coarse woody debris. Pool habitats can be particularly important for some species in arid regions where water levels decrease substantially during the summer. As central-place foragers, beaver also create early seral-stage patches that add to habitat complexity and may influence the diversity of terrestrial organisms (Naiman et al. 1988). Beaver management represents a low-cost alternative to intensive riparian rehabilitation activities, such as cabling coarse woody debris in streams, but its success depends on the ability of land managers to predict where beaver are likely to build dams and thus create pools.

Not all portions of all streams are suitable beaver habitat. Allen (1983) developed a habitat suitability index (HSI) model for evaluating lacustrine, riverine, and palustrine habitats for beaver. A similar model was developed by Urich et al. (1984) in Missouri. Howard and Larson (1985) in Massachusetts and Beier and Barrett (1987) in northern California used multivariate techniques to identify habitat features associated with beaver-occupied reaches. Slough and Sadlier (1977) developed a land capability classification system for beaver in British Columbia based on regression relationships. However, no models have been developed for beaver in arid habitats, and none of the existing models have been tested on independent data from arid habitats.

Our objectives were (1) to locate all beaver dams in a third-order basin representative of arid habitat in eastern Oregon, (2) to identify habitat features potentially important to beaver, (3) to develop a habitat classification model for beaver in the basin, and (4) to test four existing habitat classification models.

STUDY AREA

The Long Creek basin drains approximately 490 km^2 of Grant County, Oregon (Fig. 1). Elevations range from 760 to 1900 m. Average annual precipitation is 30–35 cm with most of that occurring in the winter. Temperatures range from about −10 to +30 C (Franklin and Dyrness 1973).

The area is dominated by shrub-steppe vegetation typical of arid eastern Oregon in the Blue Mountains physiographic region (Franklin and Dyrness 1973). Sagebrush (*Artemisia* spp.) dominates, with junipers (*Juniperus* spp.) and ponderosa pine (*Pinus*

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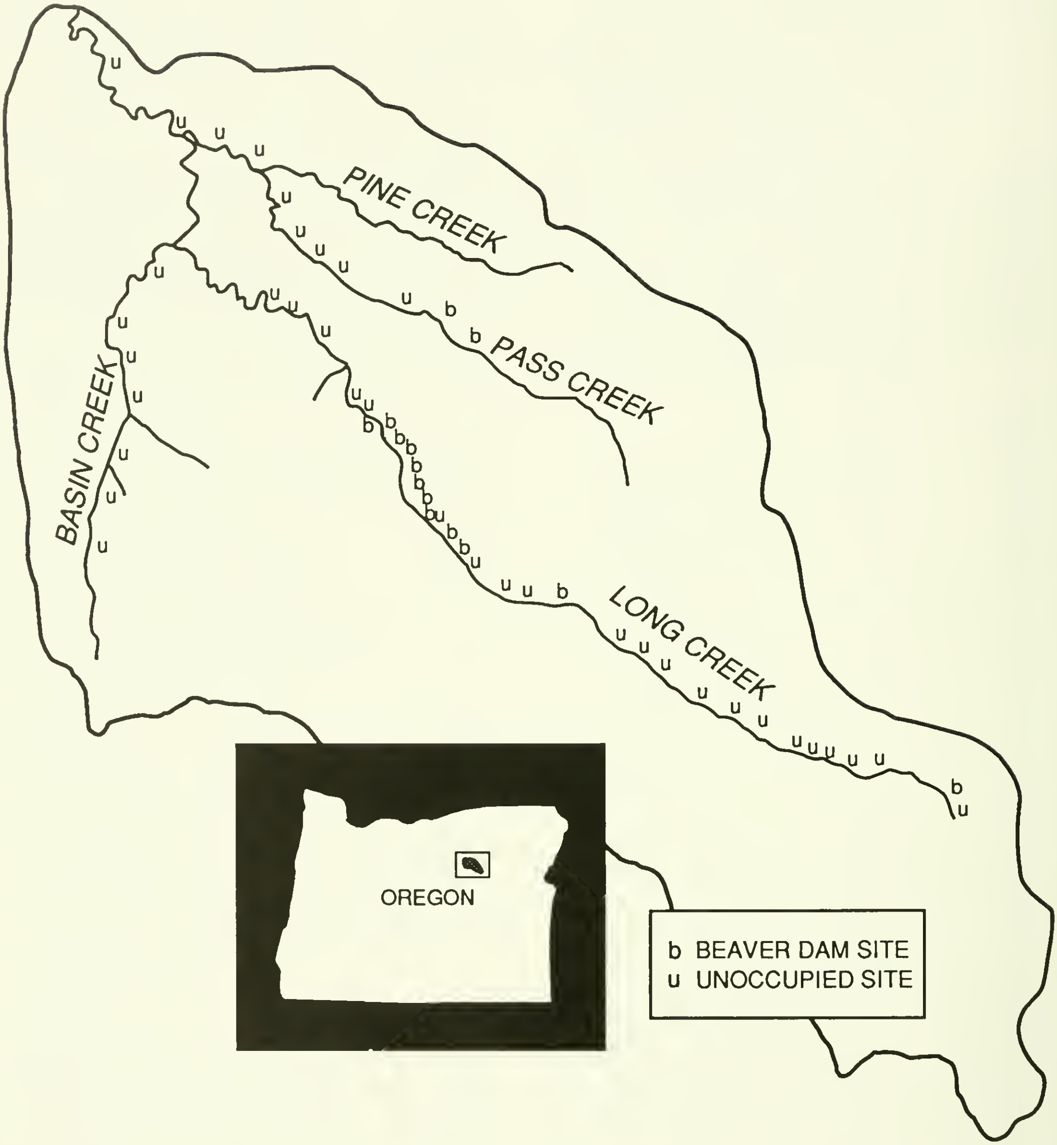

Fig. 1. Location of Long Creek basin, Grant County, Oregon, and distribution of beaver dams (b) and random unoccupied reaches (u) in the basin.

ponderosa) occurring in the higher elevations. Riparian vegetation is primarily thinleaf alder (*Alnus tenuifolia*), willow (*Salix* spp.), hawthorn (*Crataegus* spp.), and cottonwood (*Populus trichocarpa*). The dominant land use is grazing, and the land is privately owned except for the portion of the upper basin in the Ochoco National Forest.

Methods

On 2 September 1988 we examined 98 km of perennial streams in the Long Creek basin from the air at an altitude of 200–300 m. This included 48 km of Long Creek, 21 km of Pass Creek, 11 km of Pine Creek, 15 km of Basin Creek, and 3 km of unnamed streams. Thirty sites showing signs of possible beaver activity (ponds, pools, or felled trees) were marked on a topographic map and then visited on the ground. Fourteen of the possible beaver sites were actually occupied by beaver. The others were either natural pools or human-induced disturbances or structures. In September 1988 we recorded habitat characteristics at the occupied sites and at 16 randomly selected unoccupied reaches. Random reaches were selected by drawing random numbers to identify points that corresponded to distances in meters from the mouths of the streams. These reaches happened to be skewed toward the lower basin; so an additional 25 randomly selected unoccupied reaches were visited in March 1989 to obtain a better representation of riparian habitat available throughout the basin, resulting in a total of 41 unoccupied reaches.

Twenty-two habitat characteristics, including those used in previous studies, existing models, and some that were potentially important in this basin, were measured at each dam site ($n = 14$) and each unoccupied reach ($n = 41$) (Table 1). Stream variables were measured immediately below the dam at occupied sites or at the randomly selected point on unoccupied reaches. Terrestrial habitat was measured at two 40-m-diameter plots per site. Plots were established on both sides of the stream and were immediately adjacent to the dam at occupied sites or to the streambank at unoccupied reaches. Values for the two plots were averaged to characterize each site. Hall (1970) found that 90% of woody food was cut within 30 m of the stream edge, and Johnston and Naiman (in press) reported that most foraging occurred within approximately 35 m of the stream. Therefore, we assumed that 40-m-diameter plots adequately sampled terrestrial habitat for beaver. Additional variables were measured to characterize dam sites: dam height (cm), pond surface area (m^2), average basal diameters of woody stems (by species) cut by beaver, and percentage of available woody stems (by species) that had been cut by beaver.

TABLE 1. Variables measured at 14 beaver dam sites and 41 unoccupied random stream reaches in the Long Creek basin, Grant County, Oregon, 1988–1989.

Variable	Method
Stream gradient (%)	Average of gradient upstream and downstream from dam or at a random point on unoccupied reaches measured with a clinometer.
Stream width (m)	High-water width immediately below dam or random point.
Stream depth (cm)	High-water depth immediately below dam or random point.
Floodplain width (m)	Width of area dominated by alluvial soils at the dam or random site.
Bank slope (%)	Average of bank entrance angle on both sides of the stream measured with a clinometer.
Bank type	Classified as predominantly dirt or small cobble (<20 cm diameter), cobble (>21 cm diameter), or solid rock.
Distances (m)	Distance to nearest road, building, or bridge.
Drainage area (km^2)	Area drained above a dam or random point.
Plant cover (%)	Ocular estimates averaged over two 40-m-diameter plots (see text) for grasses and sedges, forbs, thinleaf alder, willow, hawthorn, cottonwood, juniper, and other conifers (mostly ponderosa pine).
Hardwood	The sum of alder, willow, hawthorn, and cottonwood covers.
Shrub	The cover of all stems <1 cm diameter.
Total canopy	The sum of hardwood and conifer covers.
Grazing pressure	Classed as low (<25% stems eaten), medium (25–50% stems eaten), high (50–75% stems eaten), or very high (>75% stems eaten).

Univariate comparisons were made between occupied and unoccupied reaches with a *t* test. Linear correlation between all combinations of pairs of variables was conducted. For pairs with $r > .80$, only the variable that seemed most biologically meaningful to beaver dam building in this basin was retained for subsequent analysis. Continuous variables were examined for normality using the *W* statistic (SAS Institute, Inc. 1982: 580). Nonnormal data were subjected to square root or logarithmic transformations to address assumptions behind parametric analysis. Any variables, either raw or transformed, with $W < 0.7$ (max $= 1.0$) were excluded from multivariate analyses. Based on these criteria, 10 of the original 20 continuous variables were retained for analysis. The subset of these

TABLE 2. Average (SE) habitat characteristics measured at beaver dam sites and unoccupied reaches, Long Creek basin, Grant County, Oregon, 1988–1989.

Habitat characteristic	Transformation	W	Occupied ($n = 14$)	Unoccupied ($n = 41$)	$P < t$
Stream gradient (%)	log	.840	2.3(0.2)	6.4(0.5)	.0001
Stream width (m)	log	.936	3.9(0.8)	3.3(0.3)	.5386
Stream depth (cm)	none	.899	5.4(0.6)	13.4(1.1)	.0001
Floodplain width (m)	log	.947	13.5(2.4)	12.0(1.4)	.5894
Bank slope (%)	sqrt	.939	11.1(2.6)	24.1(2.5)	.0009
Road distance (m)	none	.753	539 (113)	654 (68)	.3880
House distance (m)	none	.490	843 (84)	936 (24)	.2995
Bridge distance (m)	none	.473	864 (76)	903 (40)	.6332
Drainage area (km^2)	sqrt	.921	192 (23)	170 (22)	.5864
Plant cover (%)					
Grass	none	.952	54.6(5.0)	42.4(3.4)	.0669
Forb	sqrt	.894	16.8(2.3)	8.3(1.6)	.0067
Thinleaf alder	none	.631	11.2(3.7)	3.0(0.8)	.0452
Willow	none	.280	4.3(3.6)	0.9(0.3)	.3579
Hawthorn	none	.423	5.5(2.2)	1.1(0.7)	.0836
Cottonwood	none	.281	0.0(0.0)	0.0(0.0)	1.000
Hardwood	log	.904	21.0(7.1)	5.0(1.3)	.0001
Shrub	none	.650	23.1(6.7)	6.3(1.5)	.0313
Juniper	none	.198	3.6(3.6)	0.5(0.2)	.4040
Other conifer	none	.385	2.1(2.1)	1.4(0.4)	.7298
Total canopy	none	.630	26.7(8.0)	6.9(1.5)	.0001

10 variables best able to separate occupied from unoccupied reaches was selected by stepwise discriminant analysis. A classificatory model for the original data set was developed from this subset with canonical discriminant analysis.

Discrete data are reported as frequencies with chi-square goodness of fit analyses conducted for among-class comparisons. Values from random unoccupied reaches were used to establish expected frequencies.

From our data we evaluated the effectiveness of four existing habitat suitability models: (1) the U.S. Fish and Wildlife Service (USFWS) HSI model (Allen 1983), (2) the Missouri HSI model (Urich et al. 1984), (3) the Massachusetts model (Howard and Larson 1985), and (4) the Truckee River model (Beier and Barrett 1987). A new version of the Missouri HSI model includes beaver in the list of species evaluated. Scores were recorded for each occupied and unoccupied reach and then compared with a *t* test for each model. We assumed that a significant difference ($P < .05$) in scores between occupied and unoccupied reaches indicated potential utility for a model in Long Creek basin.

RESULTS AND DISCUSSION

Beaver dams were not abundant in the basin. We found an average of one beaver dam per 7 km of stream, but the distribution of the dams was highly clumped in the middle of the basin (Fig. 1). In a study covering a comparable area (600 km^2) and stream length (153 km), Beier and Barrett (1987) recorded 43 active beaver colonies in a Sierra Nevada basin. Other investigators have reported beaver dam densities of one per 0.1–3.6 km (Beier and Barrett 1987, Naiman et al. 1988).

Physical Habitat Relationships

Dam heights ($\bar{x} = 55$ cm) and pond surface areas ($\bar{x} = 167$ m^2) were highly variable (CV = 62% and 88%, respectively). Beaver dams occurred exclusively at sites with dirt rather than bedrock or cobble-dominated banks, whereas only 37% of the unoccupied reaches had dirt banks. Because beaver in this basin denned in banks or lodges adjacent to the banks, dirt substrates were probably a requisite for adequate dens.

Immediately below the dam, streams were shallower, had a gentler gradient, and had a gentler bank slope than at unoccupied reaches (Table 2). The features of dirt banks with gentle slope, low stream gradient, and relatively shallow water were best met in the middle of the basin. Further upstream the gradient was steep. Downstream the water was deep and would probably result in volumes that could wash out dams during high flows. All unoccupied reaches downstream from the occupied sites were dominated by bedrock. Drainage basin area, stream width, and floodplain width did not differ between occupied and unoccupied reaches (Table 2).

Distances to features that might have affected the likelihood of dam placement, such as bridges, roads, or buildings, did not differ between occupied and unoccupied reaches. Beaver will apparently live in close proximity to humans and human-made structures if all habitat requirements are met.

Vegetative-Habitat Relationships

Beaver cut exclusively hardwoods at the dam sites. Use of thinleaf alder (+6%), willow (−9%), and hawthorn (+3%) was nearly in proportion to availability (0% = use in proportion to availability). However, percent cover of a site by thinleaf alder was higher on occupied than on unoccupied stream reaches (Table 2). Because thinleaf alder was a dominant plant along the riparian area, hardwood cover and total canopy cover were higher on occupied than on unoccupied reaches. Alder also dominated the shrub category (stems <1 cm dbh); thus, shrub cover differed between occupied and unoccupied reaches. Cover by other potential food and dam-construction plants (willow and hawthorn) was highly variable among sites and so did not differ between occupied and unoccupied reaches, nor did cover by conifers (Table 2). Cover by forbs was higher on occupied than on unoccupied reaches, probably resulting from the higher water table around dam sites. Grass cover at dam sites did not differ from that at unoccupied reaches.

Assuming that this basin is typical of many in eastern Oregon, then beaver were most abundant prior to intensive beaver trapping in the late 1800s and early 1900s, followed by grazing of the area (Finley 1937). Kindschy (1985) reported that grazing can adversely affect beaver habitat in the region by reducing willow abundance. Grazing pressure was rated as low to none at 64% (9 of 14) of beaver dam sites and 49% (20 of 41) of unoccupied stream reaches ($X^2 = 0.73$, $P > .2$). Although we did not detect any association between grazing and dam-site selection, vegetation responses may have been obscured by historic cutting patterns of beaver, length of pond occupancy, and previous grazing practices (Kindschy 1985, Johnston and Naiman, in press). Many of the preferred food species may have been eliminated from the area prior to this study.

Habitat Classification

Bank slope, stream gradient, and hardwood canopy cover best separated ($P < .0001$, Pillai's trace = 0.62) occupied from unoccupied reaches. The model was:

$$\text{Response Variable} = 3.753 - [(\sqrt{\text{Bank slope}} * 0.272) + (\log_{10} \text{Stream gradient} * 5.239) - (\log_{10} \text{Hardwood cover} * 1.273)].$$

With zero as a decision level, negative values of the response variable were classified as beaver dam sites, and positive values were classified as random unoccupied reaches. Low values for bank slope and stream gradient and high values for hardwood cover produced negative values. The model correctly classified all dam sites and 35 of the 41 (85%) unoccupied reaches. Misclassified unoccupied reaches were dominated by either bedrock or cobble. Therefore, when all sites except those with dirt banks were deleted from the data set prior to running the model, classification was 100%. The accuracy of this model in other drainage basins of this size in eastern Oregon is unknown, but it seems likely that these habitat characteristics would influence beaver dam building elsewhere in the region.

Assessment of Existing Models

The only model that produced scores that did not differ significantly between occupied and unoccupied reaches was the Massachusetts model (Table 3). This model was designed for use in small watersheds (<750 ha) in the northeastern United States and included variables that did not pertain to conditions in eastern Oregon (soil-drainage class and abandoned-field proximity). The other three models produced scores that differed between occupied and unoccupied reaches ($P < .006$), suggesting that they can provide an index to beaver habitat quality in this basin.

Beier and Barrett (1987) used stream depth (a classificatory variable in their study) and stream gradient to identify beaver-occupied and unoccupied reaches in the Truckee River basin, California. When we assessed these

Table 3. Average (SE) scores for four models tested with data from beaver-occupied and random unoccupied reaches, Long Creek basin, Grant County, Oregon, 1988–1989.

Model	Occupied ($n = 14$)	Unoccupied ($n = 41$)	$P < t$
Massachusetts[a]	0.56(0.14)	0.52(0.06)	0.813
Truckee River[b]	1.44(0.05)	0.39(0.14)	0.001
Missouri HSI (original)[c]	0.67(0.03)	0.55(0.02)	0.006
(modified)	0.69(0.03)	0.54(0.02)	0.006
USFWS HSI (original)[d]	0.39(0.06)	0.20(0.03)	0.005
USFWS HSI (food)	1.46(0.23)	0.49(0.09)	0.001
USFWS HSI (water)	0.50(0.00)	0.43(0.02)	0.02
USFWS HSI (modified)	0.79(0.11)	0.29(0.05)	0.001
USFWS HSI (food)	1.46(0.23)	0.49(0.09)	0.001
USFWS HSI (water)	1.00(0.00)	0.78(0.05)	0.003
This study	−1.51(0.12)	1.34(0.23)	0.001

[a] Howard and Larson (1985)
[b] Beier and Barrett (1987)
[c] Urich et al. (1984)
[d] Allen (1983)

variables on the Long Creek basin data, stream gradient drove the model. The stream-depth variable was not sensitive to conditions at Long Creek. Beaver habitat suitability increased with stream depth in the Truckee River basin, but we found an opposite relationship in the Long Creek basin.

The Missouri HSI model produced acceptable results in eastern Oregon, but weaknesses were apparent. For example, this model places high habitat suitability value on stream sections with steep banks, whereas beaver in the Long Creek basin selected gentle bank slopes for dam placement. Reversing the suitability index scores for this variable made the model more sensitive to conditions in the Long Creek basin. A variable describing the proximity to croplands did not pertain to Long Creek basin and was eliminated. Making these alterations, however, changed the scores of the original model by only 0.02 units.

The USFWS HSI model produces life-requisite values between 0 and 1 for both food and water. The HSI is the minimum of these two values. The water life-requisite value is based on suitability indices (SI) for water level fluctuation and stream gradient. All sites measured in the Long Creek basin were classified as having moderate fluctuations in water level that could have influenced lodge entrances (SI = 0.5); so this variable was not sensitive to conditions at occupied and unoccupied reaches. Stream gradient was a better predictor of occupied reaches. Eliminating the variable for stream-level fluctuation from the model resulted in average life-requisite scores for water of 1.0 on occupied reaches and 0.78 on unoccupied reaches (Table 3). Average HSI scores for occupied reaches increased from 0.39 to 0.79 as a result of this change, while scores at unoccupied reaches did not change appreciably (0.20 to 0.29). We do not suggest changes in the calculation of the life-requisite value for food (and dam-construction material) because that score differed significantly between occupied and unoccupied reaches (Table 3).

Assessing Site Suitability

Williams (1965) indicated that in addition to sufficient food, suitable habitat for beavers requires a channel gradient < 15% and stable water levels. In riverine habitats, stream gradient is the most significant factor determining the suitability of habitat for beaver (Slough and Sadlier 1977). Gradient was considered an important habitat feature by Retzer et al. (1956), Slough and Sadlier (1977), Allen (1983), Urich et al. (1984), Howard and Larson (1985), Beier and Barrett (1987), and Naiman et al. (1988). Gradients on beaver-occupied reaches in the Long Creek basin ranged from 1.5 to 4.0%, while those on unoccupied reaches were as high as 12%. Excluding all stream segments with gradients >12% could facilitate identification of suitable dam-building segments along Long Creek and its tributaries. At most sites, gradients >7% are probably only of marginal value (Retzer et al. 1956). However, gradient alone is probably not the best indicator of dam-site

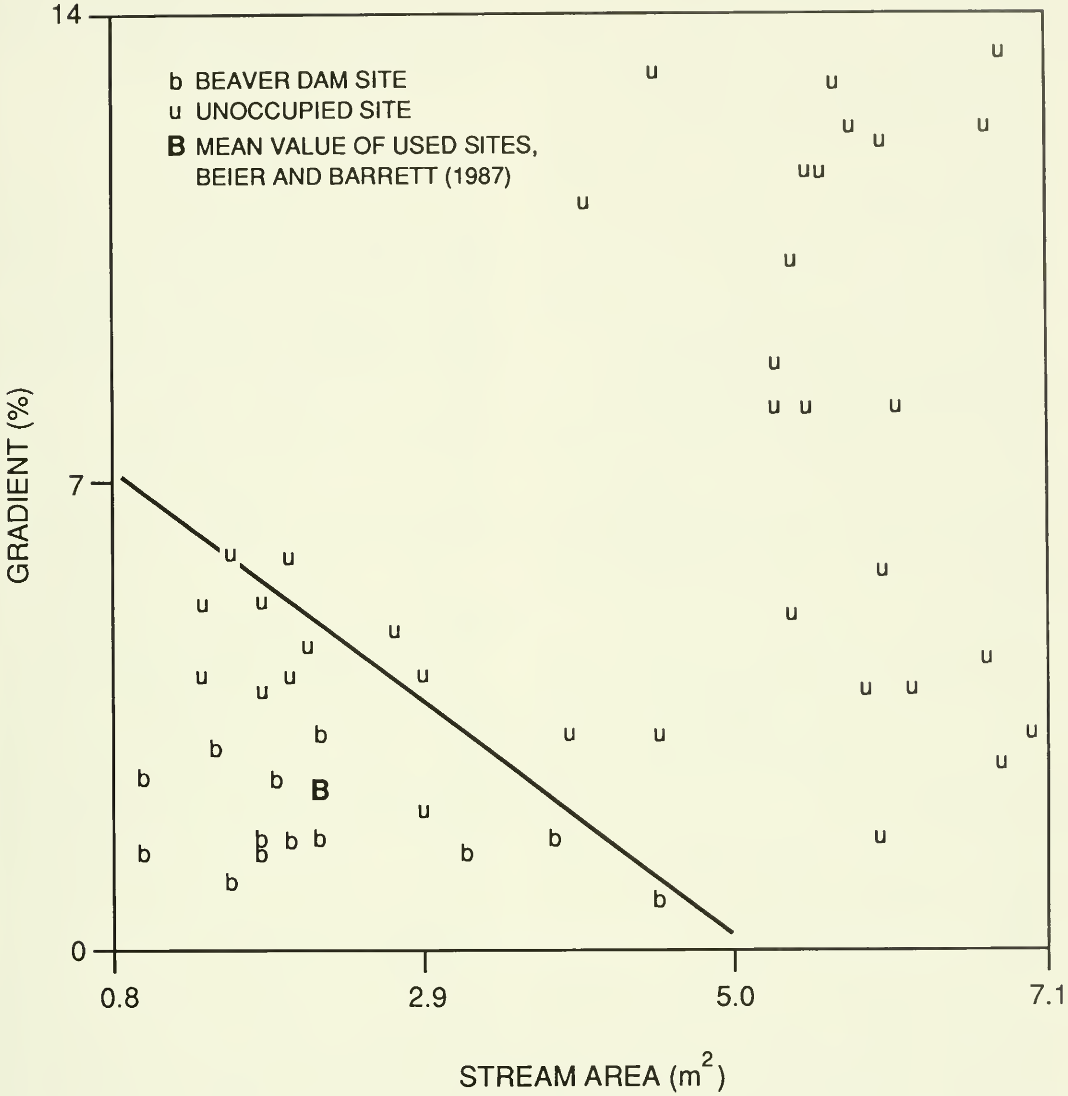

Fig. 2. Relative stream gradient diagram (stream gradient relative to stream cross-sectional area). Five random unoccupied reaches fell below 0.8-m^2 cross-sectional area. Values from random unoccupied reaches below the diagonal line were classified as unusable beaver habitat because of stream substrate or food availability (see text).

suitability. The relationship between gradient and dam building is influenced by the cross-sectional area of the stream because small, high-gradient streams can be dammed (up to a point), but large, high-gradient streams cannot. Similarly, large streams of low gradient can be dammed, but again only up to a point (~5-m^2 cross-sectional area on Long Creek). Our data support this concept, as does the mean value from active colony sites (B, Fig. 2) in the Truckee River basin (Beier and Barrett 1987). Although stream depth, width, and drainage area above the dam were important features in other studies (Howard and Larson 1985, Beier and Barrett 1987), the degree to which these variables indicate habitat quality for beaver is largely dependent on the length of stream sampled and the location of sampling in the watershed. In first- and second-order streams, these variables must be sufficiently large to provide adequate water for beaver (Howard and Larson 1985). In large streams, depth and width have a negative association with dam building because the force of the water can prevent dam persistence during high flows. Sampling a wide range of stream sizes resulted in a Gaussian distribution of these factors with similar means for occupied and unoccupied reaches (due to the location of beaver dams in the central basin), but the range of values for width and depth is narrower for occupied than for unoccupied reaches. Using relative stream gradient (cross-sectional stream area at a given gradient) overcomes this problem.

Substrate type can also be used to further refine selection of potential dam sites. Approximately 63% of Long Creek and its tributaries passes through substrates of rock or large cobble that seem to restrict dam construction. Slough and Sadlier (1977) reported that beaver in their study area did not use lakes with rocky margins.

Bank slope is another physical feature that seems important to dam-site selection. Urich et al. (1984) considered steep banks important to beaver in Missouri, probably because they offer suitable locations for dens along large streams. In our study and that of Beier and Barrett (1987) beaver were associated with gentle bank slopes. The influence of bank slope on habitat suitability may be a locally important variable and should not be universally included in habitat models.

An adequate and accessible supply of food and dam-construction materials must be present for establishment of a beaver colony (Slough and Sadlier 1977). On our study area, sites with <7% hardwood tree cover were unlikely to be dam sites (based on a 95% confidence interval). Denney (1952) summarized the food preferences of beaver in North America and reported that aspen (*Populus tremuloides*), willow, cottonwood, and alder were most often selected. The food species present may be less important in determining habitat quality than are physiographic and hydrologic factors (Jenkins 1981, Allen 1983). If food is not adequate, but the geomorphic features already described for dam placement are met, then the land manager can encourage the growth of food and dam-construction materials by restricting grazing of the riparian area, by artificial regeneration of the trees and shrubs, or both. Once a dam is built, forb abundance will probably increase (Table 2), resulting in improved food quantity and quality in the summer (Jenkins 1981).

CONCLUSIONS

For streams similar to those in the Long Creek basin, we suggest that land managers may evaluate the potential for beaver dam establishment using either the Allen (1983) HSI model modified for eastern Oregon conditions or the Beier and Barrett (1987) model. The discriminant model that we developed provided excellent classification of the original data and used habitat features identified by other investigators as important to beavers, but it has at least two weaknesses. First, variable transformations obscure direct relationships between beaver and the habitat characteristic (the square root or logarithm of a variable may not be as meaningful as the original value). Second, the model has not been tested on an independent data set.

An alternative to using the Allen (1983) or Beier and Barrett (1987) models is to use the following logic-based decision tree. A stream segment may support beaver: (1) if the relative stream gradient falls in the domain below the diagonal line in Figure 2, (2) if the stream substrate is not rock or cobble, and (3) if the hardwood cover is >7%. If hardwood cover is <7%, then the land manager has the option of improving the section of stream habitat by encouraging woody plant growth. To increase the volume of pool habitat in a stream by encouraging beaver, the land manager should identify reaches with adequate geomorphic characteristics, reestablish hardwoods (if necessary), and minimize trapping of beaver until the population is well established. For suitable stream sections, this approach would be more economical than adding logs or similar instream structures that could be better used elsewhere.

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SMALL MAMMAL RECORDS FROM DOLPHIN ISLAND, THE GREAT SALT LAKE, AND OTHER LOCALITIES IN THE BONNEVILLE BASIN, UTAH

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Collections made during 1985 and 1986 resulted in the following notes on reproduction, extensions of geographic ranges, and specimens of rare and uncommon small mammals from the Bonneville Basin in northwestern Utah. Collapsible Sherman live traps and Victor snap traps baited with a mixture of rolled oats, peanut butter, chopped raisins, and bacon fat were used for collections. Exact localities and dates of capture are reported under each species description.

Vagrant shrew (*Sorex vagrans vagrans*).—Three individuals were captured in June 1986 at Twin Springs in Tooele Co., a small spring dominated by saltgrass (*Distichlis spicata*) approximately 35 km south of Wendover, Utah (T9S, R16W). One specimen was found in an insect pitfall trap. Two additional specimens were caught 21 March 1986 in the Grassy Mountains (T3N, R11W, S26) in a shallow, narrow, dry ravine. The female contained six embryos 8 mm in length. These records extend the known range of this subspecies 35 km to the north (previous record, Durrant 1952, Ibapah, Utah) and substantiate the occurrence of this subspecies in this area of the Bonneville Basin.

Sagebrush vole (*Lagurus curtatus intermedius*).—Two females were recorded from the Grassy Mountains, near the area in which the vagrant shrews were captured. One captured 23 February 1986 was lactating and had four placental scars; the other was captured in September 1985. The latter specimen was prepared and deposited in the Department of Fisheries and Wildlife teaching collection at Utah State University. These records support the general distribution of this subspecies in northwestern Utah postulated by Durrant (1952) and establish the occurrence of the sagebrush vole in this western-central range of the Bonneville Basin. In addition, we feel it noteworthy to mention a siting of a sagebrush vole on the extreme northern Newfoundland Mountains (T6N, R13W, S17), because of the isolated nature of this range, which is surrounded by barren salt flats. The vole, observed one afternoon in June 1985, was clearly identified by its short tail and very light pelage.

Little pocket mouse (*Perognathus longimembris gulosus*).—Thirteen specimens were collected in May 1986 from the western edge of Floating Island, Tooele Co., Utah (T2N, R16W, S22), approximately 50 km northeast of Wendover, Utah, near the end of Silver Island Mountains. The site had fine sandy soil, and the dominant shrub was desert milkwort, *Polygala intermontana*. Three specimens were also collected from the north end of the Newfoundland Mountains (also reported there by H. Egoscue, personal communication). These records confirm Durrant's (1952) hypothesized distribution for this subspecies in the western deserts of Utah.

SMALL MAMMALS OF DOLPHIN ISLAND

We trapped for two nights in August 1986 when the Great Salt Lake was at a peak level of 4,212 feet above sea level. The high lake levels reduced this island to an area of <25 ha (area calculated based on the 4,210-foot contour line). A drop in lake level to 4,200 feet expands the island area to 210 ha, although much of this area is unvegetated mud flats. In 750 trap nights on the island (T9N, R10W) only *Dipodomys ordii* and *P. longimembris* were captured. This contrasts markedly with Goldman's (1939) and Marshall's (1940) censuses of the island 50 years ago. Goldman spent two nights on the island and found a much more diverse small mammal fauna in only 37 trap nights. At that time the Great Salt Lake was at a historic low, and the island was connected to the mainland by a low sandbar. Goldman reported capturing deer mice (*Peromyscus maniculatus*), ground squirrels (*Spermophilus townsendi*), and both Ord's (*D. ordii*) and chisel-toothed (*D. microps*) kangaroo rats. Also, he recorded evidence of desert woodrat (*Neotoma lepida*), coyotes (*Canis latrans*), and a carcass of a porcupine (*Erethizon dorsatum*). Goldman (1939) named a new subspecies of chisel-toothed kangaroo rat (*D. m. russeolus*) and Ord's kangaroo rat (*D. o. cineraceus*), based on specimens he captured on the island.

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We saw sign of runways of *S. townsendi* through dense stands of cheatgrass, although we saw no aboveground activity in August when we visited the island. In addition, we saw droppings and weathered nests of *Neotoma*, but none of them were recent, suggesting that there may be no woodrats left on this island. While no live lagomorphs were observed on the island, two weathered, disarticulated skeletons of jackrabbits (*Lepus* sp.) were also found, but these could have been carried there by raptors. The island almost certainly has no *Peromyscus* remaining. In other west desert areas we would normally catch a minimum of 10–15 deer mice for 750 trap nights of effort even in very poor habitat such as the cheatgrass (*Bromus tectorum*) monoculture dominating the island. We caught no specimens of *D. microps* and believe that the subspecies named for its occurrence on the island, *D. m. russeolus*, is extinct.

Ord's kangaroo rat (*Dipodomys ordii marshalli*).—We captured 11 individuals of this subspecies. Five specimens were deposited in the National Museum of Natural History and another five reside in the University of Utah Museum of Natural History.

The specimens of Ord's kangaroo rat do not appear to fit within the range of variation for *D. o. cineraceus*, the subspecies first described by Goldman (1939) as endemic to Dolphin Island. Our specimens are much darker than *cineraceus*, particularly the tails. In addition, all of our specimens have black facial markings like the mainland subspecies, *D. o. marshalli*. Only one specimen from the original series of *cineraceus* has these markings (personal communication, Don Wilson, U.S. Biological Survey). However, our specimens are not identical to *marshalli*; they are slightly paler and the tails are darker than *marshalli*. The skulls of all specimens are very similar. These comparisons of our specimens with the original series (collected by Goldman) were confirmed by comparisons to specimens of *D. o. marshalli* at the University of Utah Museum of Natural History. Thus, we feel that our specimens of *D. ordii* collected on Dolphin Island are more closely related to the subspecies *D. o. marshalli* than to the original subspecies *D. o. cineraceus* described by Goldman (1939). Durrant (1952) earlier questioned the validity of subspecific status for *cineraceus*, noting frequent connection of Dolphin Island with the mainland and a lack of nearby mainland specimens.

Little pocket mouse (*Perognathus longimembris gulosus*).—Six specimens of the little pocket mouse were collected on Dolphin Island. This species has not been recorded previously from any island in the Great Salt Lake (Goldman 1939, Marshall 1940, Bowers 1982). Few records are available for this species in the Bonneville Basin (Durrant 1952, Shippee and Egoscue 1968), the nearest from Kelton, Utah, on the north shore of the lake. Trapping on the nearby mainland at higher elevations (5,500 feet) in the Hogup Mountains failed to produce any individuals of this species. This may have been due to the absence of habitats usually preferred by this species. The *P. longimembris* specimens collected on Dolphin Island are much darker overall than *gulosus* (although still within the range of variation of this subspecies) but appear identical in skull morphology. Specimens examined from Dolphin Island are deposited in the National Museum of Natural History (3) and the University of Utah Museum of Natural History (3).

The complete isolation of the island from the mainland for several years probably explains these faunal changes. High lake levels have inundated formerly choice dune habitats occupied by the heteromyids that still persist on the island. It is likely that the island fauna has changed repeatedly over the years as a result of lake level fluctuations that alternately isolated it from and connected it with the mainland. In the 1900s alone, the island has been isolated from and reconnected to the mainland on at least three separate occasions (Gwynn 1980). This could account for the apparent reinvasion of the island by *D. o. marshalli* and possible swamping of variation found in the subspecies *cineraceus*. Frequent and periodic invasions and subsequent isolation make Dolphin Island a very dynamic system whose mammalian fauna could change dramatically as often as lake levels fluctuate with varying precipitation patterns. Major changes include the extinction of a unique subspecies (*D. m. russeolus*) and the potential creation of a new subspecies of little pocket mouse.

Whereas Marshall (1940) recorded seven species of mammals on Dolphin Island when it was connected by a narrow sandbar to the mainland, now apparently only two small mammal species, *Dipodomys ordii* and *Perognathus longimembris*, survive, with possibly a third species, *Spermophilus townsendii*, surviving as well.

ACKNOWLEDGMENTS

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TWO PRONGHORN ANTELOPE FOUND LOCKED TOGETHER DURING THE RUT IN WEST CENTRAL UTAH

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American pronghorn antelope (*Antilocapra americana americana* Ord 1818) bucks begin showing signs of entering the rutting period in late August in western Utah (Smith and Beale 1980). Bucks exhibit territorial dominance by marking vegetation with subaricular gland secretions, urine and feces, and by direct interactions with other bucks (Kitchen 1974, Yoakum 1978). This territorial behavior assures that the larger, healthier males do the majority of the breeding (Kitchen 1974). Often fights between bucks result in injury (Kitchen 1974); on rare occasions these fights have resulted in the deaths of male mule deer (Geist 1981) and white-tailed deer (Marchinton and Hirth 1984) when their horns have become locked together. The occurrence of pronghorn bucks locking together as a result of fighting has been documented very few times. Spencer (1942) reported a case in South Park, Colorado, in which the right horn of one buck pierced the underside of the second buck's jaw while its left horn locked behind the second buck's right horn. Yoakum (personal communication, 1988) reported that two bucks with interlocked horns were found dead on the Hart Mountain National Wildlife Refuge in Oregon during the late 1940s.

On 17 September 1986 a rancher from Sutherland, Utah, found two dead pronghorn bucks locked together. The pair were found approximately 10 km west of Sand Mountain in Juab County, Utah (T14S, R6W, Sec. 9.). This area is flat saltbrush desert, and dominant vegetation species include black greasewood (*Sarcobatus vermiculatus*) and shadscale (*Atriplex confertifolia*). One buck had heart-shaped horns, 39.4 cm in length, with inward curving tips 3.8 cm apart. During the fight this buck evidently thrust its horns upward on the underside of the second buck's neck; the horn tips flexed far enough apart to allow the second buck's neck to pass through. The horns were then locked around the second buck's neck. The second buck's neck was rubbed raw and heavily scabbed, indicating that the two animals may have remained locked together for some time before dying.

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MICROBIOLOGY AND WATER CHEMISTRY OF TWO NATURAL SPRINGS IMPACTED BY GRAZING IN SOUTH CENTRAL NEVADA

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This study was initiated to monitor the water chemistry and microbial populations at two sites in southern Nevada: Ash Springs and Condor Canyon. Cattle impact was suspected to be a causative factor in increased mortality of two endangered fish species: White River springfish (*Crenicthys baileyi baileyi*) in Ash Springs and Big Spring spindace (*Lepidomeda mollispinis pratensis*) in Condor Canyon.

Condor Canyon, located at the northern end of the Meadow Valley Wash in south central Nevada, is approximately four miles long and contains a stream system that runs alternately through Bureau of Land Management and private land. Site 1 is furthest downstream near the bottom of the canyon. Site 2 is within the canyon, and site 3 is near the mouth of the canyon, adjacent to the spring source. Site 4 is closest to another spring source on Delmues's Ranch, a private ranch where cattle currently graze. Cattle are also occasionally present near site 3.

Ash Springs, in Pahranagat Valley, is a warm-water spring with temperatures varying from 33 C to 35 C. Between summer of 1986 and spring of 1987 cattle were present at the headpool, and there was a marked decline in springfish and other endemic species. Removal of the cattle by fencing (initiated by the BLM in 1987) allowed fish numbers to increase to the same levels as prior to the decline (Taylor et al. 1990). Because of the recovery, this area served somewhat as a control, but residual manure continues to influence the spring whenever precipitation occurs. The headpool is still utilized by the public as a "hot tub."

Collection trips were planned for both spring sites on a monthly basis beginning in September 1988 and continuing until August 1989. We gathered water samples from four sites in Condor Canyon and two sites at Ash Springs with duplicate samples taken from one site each month on a rotational basis. Weather conditions, water levels, and flow were monitored by ocular estimation. Water and air temperatures were taken using a calibrated thermometer. Conductivity (Corning, model PS-17), pH (Hanna Instruments, model 0624-00), and dissolved oxygen (Hach) were tested in the field using calibrated equipment. Water was collected in sterile Nalgene bottles by hand-dipping the bottle, rinsing, and refilling without sampler-related contamination.

Total bacterial counts were evaluated by dilution and spread plating on R2A agar (Difco) as well as by membrane filtration (Gelman GN6) during the winter months when counts were low. Plates were incubated at room temperature for five to seven days.

Total coliforms were measured using the most probable number method (MPN) (American Public Health Association 1985) and membrane filtration followed by growth on mEndo agar (Difco) at 37 C. Fecal coliforms were also cultured after membrane filtration and support on mFC agar (Difco) at 44 C. Each coliform colony and positive MPN tube was confirmed by inoculation into Brilliant Green Bile Broth (Difco) tubes, and each was scored positive when gas and acid were produced.

Pseudomonas aeruginosa and *Aeromonas hydrophila* were also evaluated by membrane filtration. Bacteria on the filters were grown on mPA agar (American Public Health Association 1985) at 41 C for isolation of *P. aeruginosa*. Positive colonies were confirmed by streaking on skim milk agar with clearing of the milk by colonies. MacConkey agar (Difco) was originally used for enumeration of *A. hydrophila*, but it did not clearly select for that organism. A comparison of several selective

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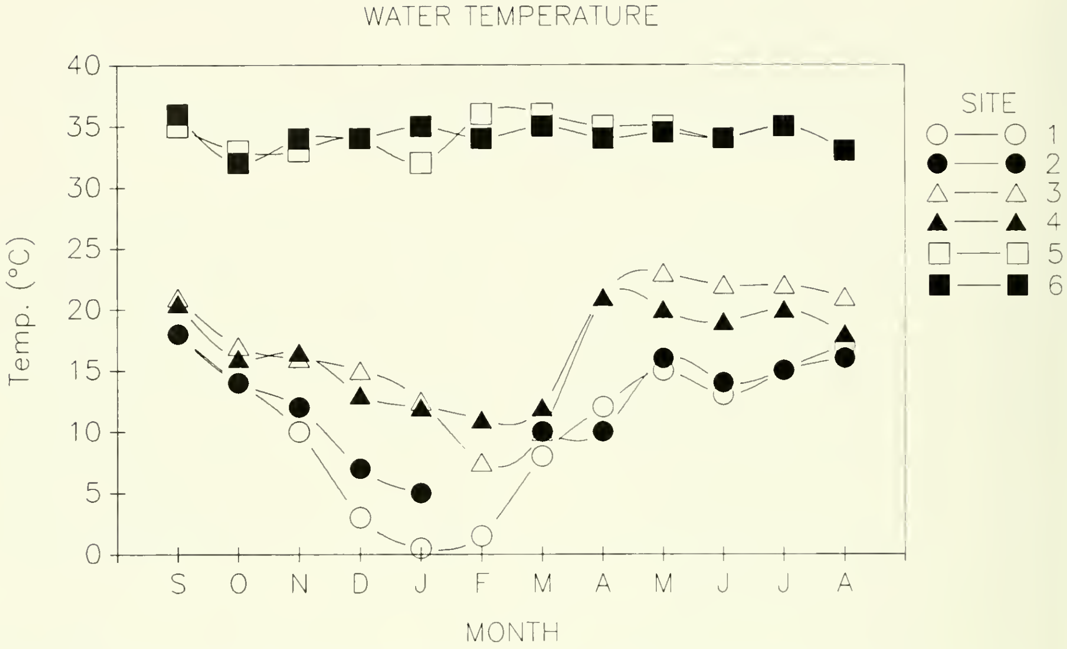

Fig. 1. Water temperatures in Ash Springs and Condor Canyon. Sites 1–4 were in Condor Canyon and sites 5 and 6 at Ash Springs.

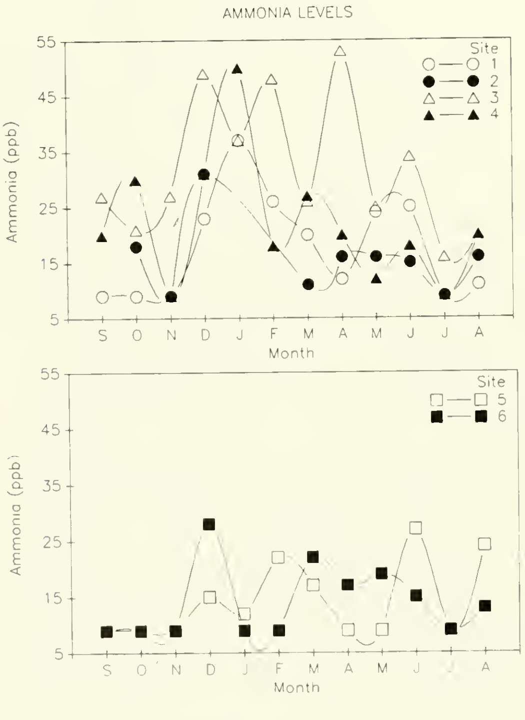

Fig. 2. Ammonia levels in parts per billion. Top frame depicts Condor Canyon, bottom frame Ash Springs.

media for enumeration of *A. hydrophila* by Arcos et al. (1988) found mA agar (Rippey and Cabelli 1979) to be the most effective; therefore, we replaced the MacConkey agar with mA agar beginning with the November sampling. Incubation was carried out at 37 C, and suspected positive colonies (denoted by a yellow color) were inoculated into AH semisoft agar tubes (Kaper et al. 1979). A positive reaction was scored in tubes exhibiting alkaline conditions at the top and acid production at the butt of the tube. Confirmed organisms were motile, produced indole, and did not produce hydrogen sulfide.

Water temperatures in Condor Canyon exhibited a gradient with higher temperatures at sites 3 and 4 near the source of the springs and cooler temperatures within the canyon. Temperatures in the canyon dropped during the winter months and increased again during the summer, while in Ash Springs they remained stable throughout the year (Fig. 1).

The ammonia levels in Condor Canyon fluctuated throughout the year, but a general increase was observed during December and January, along with a less significant increase in June (Fig. 2). Sites 5 and 6 at Ash Springs exhibited a similar pattern during these months.

When the nitrate plus nitrite levels were graphed together, a pattern similar to the NH_3 data was seen, but there was a lag time of nearly a month in the peaks for both Condor Canyon and Ash Springs (Fig. 3). There was a nitrate plus nitrite gradient in the Condor Canyon sites, with site 4 at the top of the canyon being highest and site 1 at the bottom lowest.

A large peak in organic phosphorus (OP) levels during March correlated with NH_3 peaks observed during that month. Ash Springs and Condor Canyon both exhibited this phenomenon (Fig. 4).

Total viable counts in Condor Canyon were dramatically similar to OP levels during March (Fig. 5). The peak at site 2 in January was notable. At Ash Springs total counts varied little. A slight peak was observed in March, but this may not be statistically valid.

Pseudomonas aeruginosa, an opportunistic fish pathogen, was found on a regular basis only at site 5 in Ash Springs, with rare colonies appearing at site 6. A pattern similar to that exhibited in the total viable counts can be seen, with a dramatic peak in March and also with higher numbers during the summer and early fall (Fig. 6).

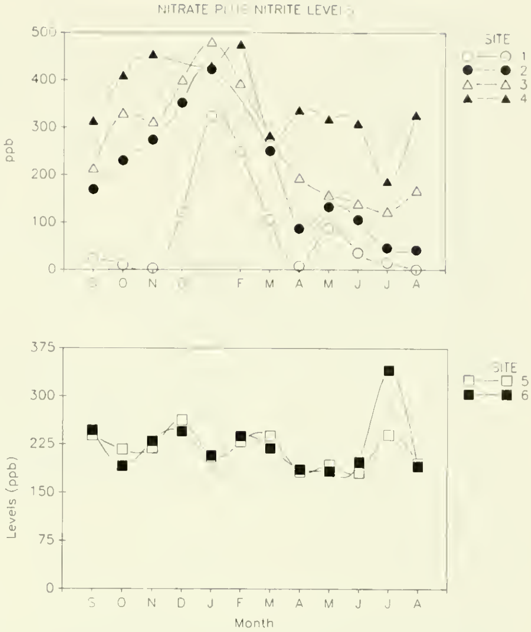

Fig. 3. Nitrate plus nitrite levels in parts per billion. Top frame depicts Condor Canyon, bottom frame Ash Springs.

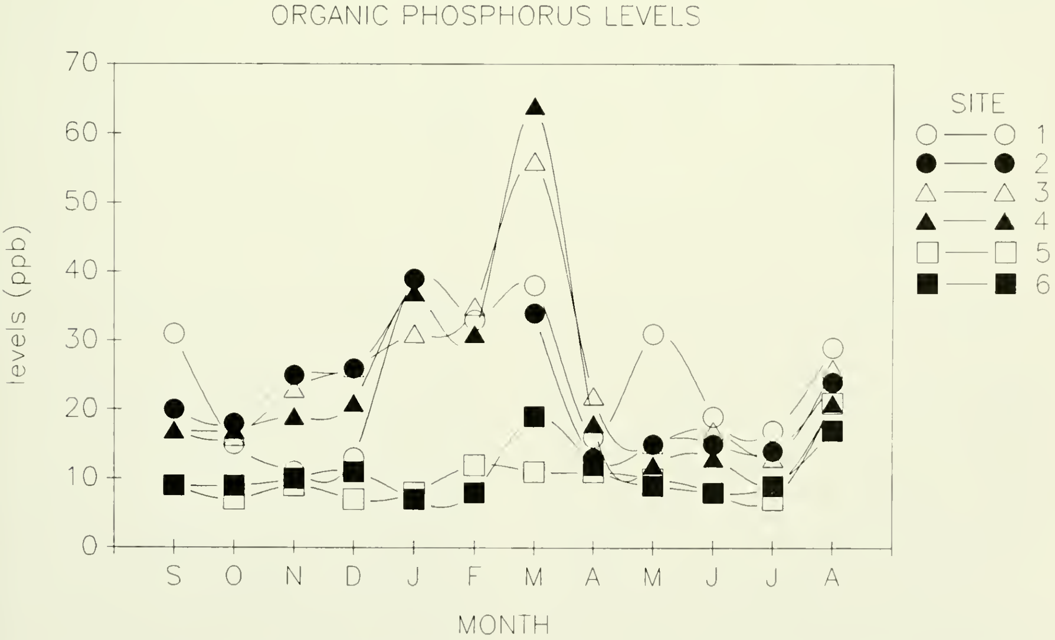

Fig. 4. Organic phosphorus levels in parts per billion. Sites 1–4 were in Condor Canyon, sites 5 and 6 at Ash Springs.

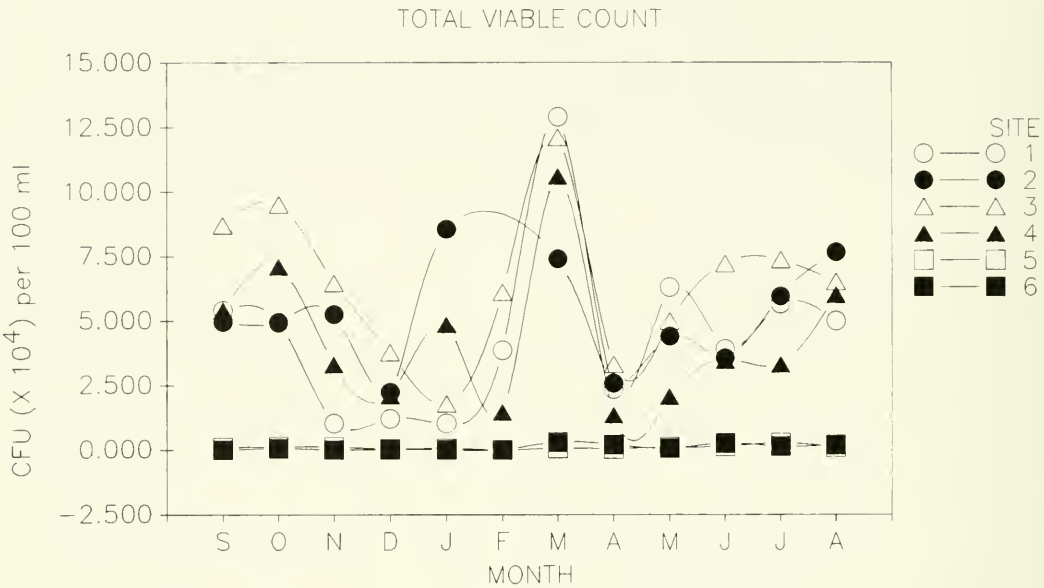

Fig. 5. Total viable counts in colony-forming units per 100 ml. Sites 1–4 were in Condor Canyon, sites 5 and 6 at Ash Springs.

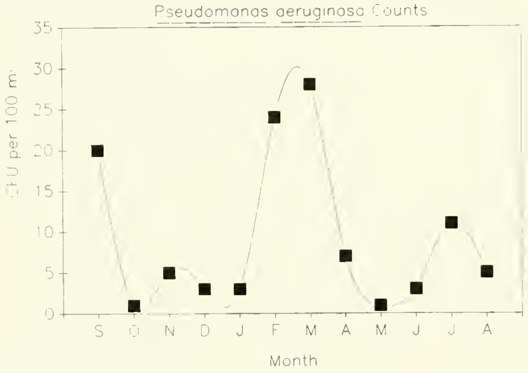

Fig. 6. *Pseudomonas aeruginosa* counts in colony-forming units per 100 ml at site 5 in Ash Springs.

Aeromonas hydrophila, another opportunistic fish pathogen, was found at all sites. Colony-forming units (CFU) in Ash Springs followed the pattern seen with *Pseudomonas aeruginosa* levels, showing peaks in March and July (Fig. 7). In Condor Canyon a slight peak was also observed in March, with increased numbers during the summer months when total microbial counts were also higher.

The shape of the graph of total coliform levels in Condor Canyon (Fig. 8) is similar to the graph of total viable bacterial CFU (Fig. 5). Fecal coliforms were elevated in March, and Figure 9 markedly resembles the graph of total viable counts (Fig. 5). The peak at site 2 in January appeared also.

The increase of ammonia levels in Condor Canyon during December, January, and June correlated with precipitation and cattle presence in the canyon. Rain and snow were abundant in December and January, with the additional summer showers typical of the Mojave Desert occurring in June. Cattle were present at site 3 in December, and the streambanks were trampled in January. When cattle were present, they deposited NH_3 in the form of urine and feces, and runoff during winter rainstorms washed additional nitrogen into the system from residual feces. Because nitrogen is often a limiting nutrient in ecosystems, monitoring nitrogen-containing chemical species is important. The peaks in nitrogen species at sites 5 and 6 (Ash Springs) in December and June were probably due to precipitation rather than cattle presence (Fig. 2). A peak was also noted there during March. (It was raining during this sampling trip.)

The lag time observed between the higher ammonia and nitrite plus nitrate levels was most likely due to the oxidation of ammonia through nitrite to nitrate (Fig. 3). This most often occurs as a metabolic process of nitrifying bacteria, and this conversion can become slower in cool temperatures and when low numbers of nitrifying bacteria are present.

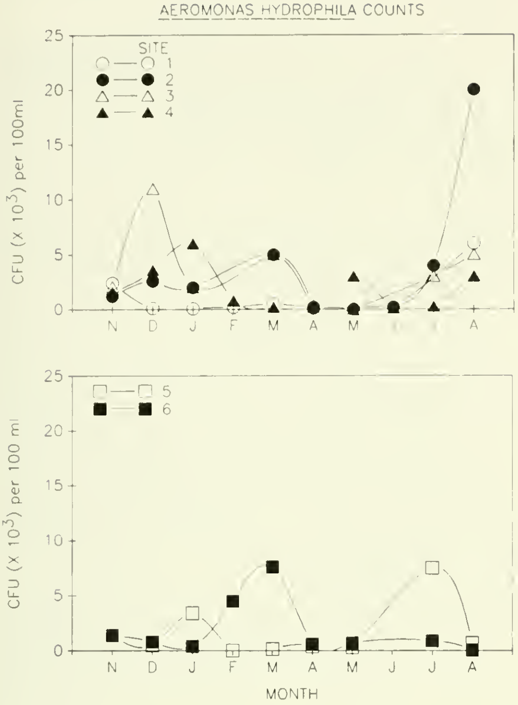

Fig. 7. *Aeromonas hydrophila* counts in colony-forming units per 100 ml. Top frame depicts Condor Canyon, and bottom frame depicts Ash Springs.

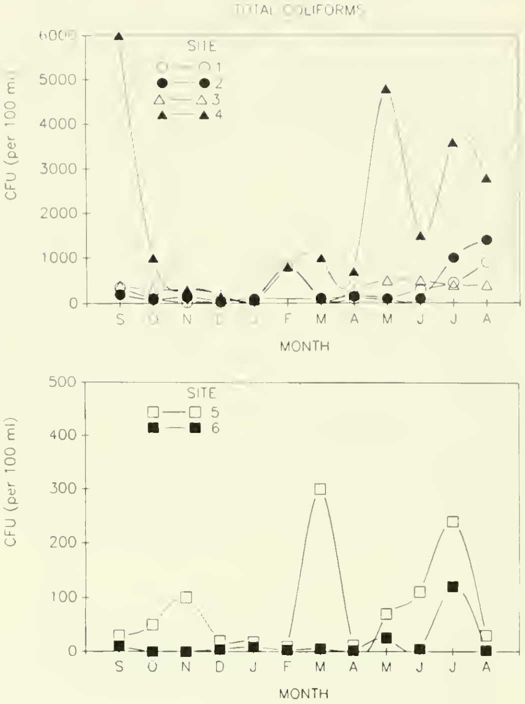

Fig. 8. Total coliform counts in colony-forming units per 100 ml. Top frame depicts Condor Canyon, and bottom frame depicts Ash Springs.

The elevated level of total viable bacteria during March was probably due to the availability of OP and other nutrients washed in by the rain from both feces and any fertilizers used by the nearby rancher (Figs. 5, 6). At other times bacterial growth was probably limited by lack of phosphate. The higher counts in summer and early fall are likely due to the warmer water temperatures in Condor Canyon. At Ash Springs, where water temperature remained stable, total counts varied little. *Pseudomonas aeruginosa* levels followed a similar pattern although they were found only in Ash Springs.

Figure 7 depicts *Aeromonas hydrophila* data beginning with November and extending through August only because of the change in the isolation medium explained above.

On the total coliform graph (Fig. 8) the peaks from February through March in Condor Canyon again probably reflect precipitation. The significantly higher numbers at site 4 during the warmer months correlate with the time periods when cattle were most prevalent and water was slowest and warmest. At Ash Springs the numbers of coliforms reflected precipitation rather than cattle presence, as exhibited by the peaks in March and July when precipitation occurred. There had been no cattle access to Ash Springs for six months prior to the beginning of this study, but the effect was still seen during times of sufficient precipitation. Increased fecal coliform numbers were similarly observed during the rainy season and when water temperature was warmest in Condor Canyon (Fig. 9).

As expected prior to this study, bacterial levels were influenced by water temperatures, with higher counts correlating with warmer water. In Condor Canyon increased numbers reflected these changes during the warmer months, while in Ash Springs they remained fairly stable throughout the year. Bacterial levels also reflected increased precipitation and cattle presence because of the influx of nutrients necessary for growth of microorganisms. Influence of cattle could be seen months after their physical presence when precipitation allowed an influx of nitrogen and phosphorus.

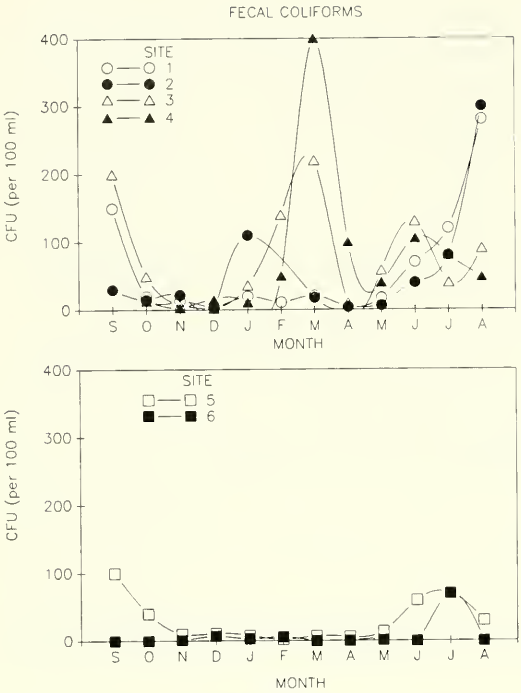

Fig. 9. Fecal coliform counts in colony-forming units per 100 ml. Top frame depicts Condor Canyon, and bottom frame depicts Ash Springs.

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BIRDS OF A SHADSCALE (*ARTRIPLEX CONFERTIFOLIA*) HABITAT IN EAST CENTRAL NEVADA

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Despite widespread distribution of shadscale (*Atriplex confertifolia*) habitat in the Great Basin Desert (Fowler and Koch 1982), it has been largely ignored by avian ecologists. There are few quantitative assessments of breeding bird populations in these vast areas used primarily for livestock grazing (but see Fautin 1946 for western Utah, Smith et al. 1984 for southwestern Idaho). This information is basic to understanding the ecology of desert birds and the stewardship of their habitats. In this paper I describe breeding bird densities of a shadscale community in the Snake Valley of east central Nevada and compare them with other quantitative studies from shadscale habitats.

Study Area

The study area is located 4 km north of Baker in southeastern White Pine County, Nevada, at a median elevation of approximately 1600 m. The study area is a flat valley bottom bounded by foothills and mountains; there are no seeps, springs, or live streams on the site, although dry washes cross the valley floor. Climatically, the area is a cold desert with cold winters and hot, dry summers. Maximum temperatures in summer frequently exceed 35 C, and minimum temperatures in winter often drop to −29 C (Houghton et al. 1975). Annual precipitation ranges from 10 to 20 cm (Houghton et al. 1975). The area is grazed lightly by cattle trailing to and from spring-fall ranges (R. Jenson, personal communication).

Vegetation in the study area comprises a mixture of low shrubs with a sparse herbaceous component. Dominant shrubs are shadscale, green molly (*Kochia americana*), common winterfat (*Eurotia lanata*), bud sagebrush (*Artemisia spinescens*), and spiny hopsage (*Grayia spinosa*). Fourwing saltbush (*Atriplex canescens*), black greasewood (*Sarcobatus vermiculatus*), and rubber rabbitbrush (*Chrysothamnus nauseosus*) occasionally occur along shallow washes. Three perennial grasses, Indian ricegrass (*Oryzopsis hymenoides*), galleta (*Hilaria jamesii*), and squirreltail (*Sitanion hystrix*), occur throughout the site. Cheatgrass (*Bromus tectorum*), an annual, is a frequent associate. Plant names follow Holmgren and Reveal (1966).

Methods

A 20-ha plot was censused for breeding birds using the spot-map method (International Bird Census Committee 1970). A census plot, chosen as the best representative of the shadscale community, was selected by examining the vegetation and topography of the general area. A square plot was surveyed and gridded with points numbered and marked with stakes at 75-m intervals. Ten census visits to the plot were made annually from 29 March to 1 June from 1981 to 1983. Most spot mapping was done from sunrise to early afternoon when birds were most active. Different census routes through the plot were used, with different starting and ending points distributed as evenly as practicable among the visits. To ensure complete coverage, the plot was censused by walking within 50 m of all points on the grid. Recorded bird observations extended a minimum of 75 m beyond plot boundaries.

At the end of the sampling period, clusters of observations and coded activity patterns on species maps were circled, indicating areas of activity or approximate territories. Fractional parts of boundary territories were determined by estimating the portion of each edge cluster that fell within the study plot. Oelke (1981)

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TABLE 1. Passerine breeding bird densities (individuals/ha) in shadscale vegetation, east central Nevada, 1981–1983.

Species	Foraging category[a]	Nesting substrate[b]	Breeding bird density 1981	1982	1983
Horned Lark (*Eremophila alpestris*)	GGO	G	1.28	1.52	1.32
Brewer's Sparrow (*Spizella breweri*)	GGI	B	0.08	0.10	0.08
Sage Thrasher (*Oreoscoptes montanus*)	GGI	B	0.02	+[c]	0.05
	Total individuals/ha		1.38	1.62	1.45
	Biomass (g/ha)[d]		42	49	44
	Species richness (n)		3	2	3

[a] After DeGraaf et al. (1985): GGO = ground gleaning omnivore, GGI = ground gleaning insectivore.

[b] After Harrison (1979): G = ground nester, B = bush nester.

[c] + indicates the species was observed infrequently (less than three registrations).

[d] Species weights from Dunning (1984).

and Verner (1985) summarized methodological and other special problems of the mapping method.

Total bird biomass was calculated annually by summing the products of breeding bird species densities and average bird species body weights (Dunning 1984). Bird nomenclature is from the 1983 AOU check-list (American Ornithologists' Union 1983).

RESULTS AND DISCUSSION

Three passerine bird species bred on the study site (Table 1). By far the most common breeder was the Horned Lark (*Eremophila alpestris*). A permanent resident, this broadly distributed bird occurred throughout the study plot. Less common, and in more restricted locations, were two summer residents, the Brewer's Sparrow (*Spizella breweri*) and the Sage Thrasher (*Oreoscoptes montanus*).

Other species, observed as occasional visitors on or over the study plot during the breeding season, included Northern Harrier (*Circus cyaneus*), Red-tailed Hawk (*Buteo jamaicensis*), Ferruginous Hawk (*Buteo regalis*), Golden Eagle (*Aquila chrysaetos*), American Kestrel (*Falco sparverius*), Prairie Falcon (*Falco mexicanus*), Mourning Dove (*Zenaida macroura*), Burrowing Owl (*Athene cunicularia*), Short-eared Owl (*Asio flammeus*), Violet-green Swallow (*Tachycineta thalassina*), Cliff Swallow (*Hirundo pyrrhonota*), Barn Swallow (*Hirundo rustica*), Common Raven (*Corvus corax*), Loggerhead Shrike (*Lanius ludovicianus*), Vesper Sparrow (*Pooecetes gramineus*), Black-throated Sparrow (*Amphispiza bilineata*), and Western Meadowlark (*Sturnella neglecta*).

Horned Lark breeding territories were contiguous on the study plot. From 91% to 95% of the total bird density each year was accounted for by the Horned Lark (Table 1). This species inhabited areas in which the vegetation was open and low growing with considerable bare ground. Horned Larks sang from the ground, while perched, or from the air during nuptial flight displays. Five Horned Lark nests were found during the study; all were placed on the ground in shallow excavations partly beneath or beside a low shrub or grass tussock. Incubating females were first observed on 22 April 1983 and nestlings were last observed on 19 May 1983.

In the Great Basin, Horned Larks are usually most abundant in arid valleys but may occur in suitable habitat on mountain plateaus or in montane fields (Ryser 1985) as well as in cold northern desert scrub, sagebrush, and subalpine grasslands (Behle and Perry 1975).

Brewer's Sparrows were a consistent but relatively minor avian component of the shadscale community in this study (Table 1). As a breeding bird it was largely restricted to scattered clumps of black greasewood, fourwing saltbush, and rubber rabbitbrush occurring near a shallow dry wash that crossed the study site. I found no nests of Brewer's Sparrow but observed singing, courtship, pairing, and other breeding activities. This sparrow normally breeds in big sagebrush (*Artemisia tridentata*) habitats but will also nest in a variety of other suitable shrubs (Short 1984).

TABLE 2. Breeding bird densities (individuals/ha) in shadscale communities of the Great Basin Desert.

Location	Year	Total density	Species	Reference
Southwestern Idaho[a]	1979	1.54	3+	Smith et al. 1984
	1980	1.54	3+	" " "
Southwestern Utah	1984	1.38	2	Medin 1986
	1984	1.39	2	" "
	1984	0.98	3	" "
	1984	1.16	3	" "
Western Utah	1940	1.06	3	Fautin 1946
East central Nevada	1981	1.38	3	This study
	1982	1.62	2	" "
	1983	1.45	3	" "

[a] Identified as the salt-desert shrub vegetation type. Shrub species included shadscale, bud sagebrush, common winterfat, black greasewood, fourwing saltbush, Nuttall saltbush (*Atriplex falcata*), and littleleaf horsebrush (*Tetradymia glabrata*).

I recorded relatively low densities of Sage Thrashers in the shadscale community. Sage Thrashers bred on the study plot only two of the three study years (Table 1). Mapped breeding territories included the tallest black greasewood shrubs associated with the dry wash that crossed the area. Sage Thrashers were not common on the study plot, and no nests were found. Although considered by some investigators to be a sagebrush obligate (e.g., Braun et al. 1976), Sage Thrashers occur in other plant communities. Behle and Perry (1975) list the Sage Thrasher as a regular but relatively uncommon bird of the Great Basin desert scrub formation that includes shadscale, black greasewood, and rubber rabbitbrush. Fautin (1946) classified the Sage Thrasher as a summer resident in greasewood habitats of western Utah.

Few other assessments of breeding bird densities in shadscale habitats are available (Table 2). Fautin (1946: 287) reported an average summer population, from actual counts on 4-ha plots, of 1.06 birds/ha in shadscale communities of western Utah. Nesting birds included Horned Larks, Rock Wrens (*Salpinctes obsoletus*), and Black-throated Sparrows. Medin (1986: 570) found total densities ranging from 0.98 to 1.39 birds/ha on several sample plots on the Desert Experimental Range in southwestern Utah. Breeding birds included Horned Larks, Black-throated Sparrows, and Loggerhead Shrikes. Smith et al. (1984: 263) reported a total density of 1.54 passerine birds/ha in a salt-desert shrub community in southwestern Idaho.

Results from my three-year study of breeding bird populations in a shadscale habitat in east central Nevada were numerically similar to those from shadscale habitats elsewhere in the Great Basin Desert. Overall, the number of bird species breeding on a census plot in shadscale habitats ranged between two and three. Breeding bird densities in shadscale habitats were relatively uniform between years and locations, ranging from 0.98 to 1.62 individuals/ha. But there were pronounced compositional differences in the breeding bird communities. Of several bird species reported breeding in shadscale habitats, only the Horned Lark was common to each census plot. Observed differences in the composition of breeding bird communities may have been related to physiognomic and floristic differences in the vegetation at each location.

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CALIFORNIA GULL POPULATIONS NESTING AT GREAT SALT LAKE, UTAH

Don S. Paul[1], Joseph R. Jehl, Jr.[2], and Pamela K. Yochem[2]

Although the California gull (*Larus californicus*) is the state bird of Utah, the history and status of colonies nesting at Great Salt Lake have not been well documented. Stansbury (1852) reported gulls nesting in 1850, and the population has been studied sporadically since then. Behle (1958: 22–32) provided a comprehensive review of the history of the colonies and commented on the reliability of early estimates, many of which were greatly exaggerated. He made the first complete survey in 1931 (Behle 1958: 23), reporting approximately 80,000 adults breeding on the Great Salt Lake islands. Behle (1958: 32) continued to study the population through the 1950s and concluded that

> the only generalization one can make is that there are population shifts constantly going on and there seems to be a movement from the remote colonies of the lake eastward, closer to the foot of the Wasatch Front and closer to the food supply. . . . It is not certainly known whether there has been an actual increase of the total population of gulls for the entire region during late years as some claim. It is my feeling that such is not the case. Rather, by moving their nesting colonies to new locations to the east or at the several refuges, the seagulls are more conspicuous.

Behle (1958: 32) provided several examples of relocations, most notably:

> Hat Island which once supported 20,000 gulls has been completely abandoned and the Gunnison Island population has been reduced from 60,000 to 10,000 or 15,000. In contrast, the Rock Island [Utah Lake] colony increased from a few hundred to 27,850.

Sporadic records and unequal effort make data from 1932 through 1981 difficult to interpret. To gain a better understanding of the current situation, the Utah Department of Natural Resources, Division of Wildlife Resources (DWR), repeated Behle's work by conducting aerial and ground censuses of the colonies in 1982 and 1983 (Paul 1983). Additional surveys were made in 1986, 1987, and 1989 (Paul 1986, 1987, 1989). In all years, the location of the colonies was determined by making an aerial survey of the entire lakeshore and the islands. In 1982 and 1983 a walk-through strip count of active nests and young was the primary method used to determine colony size: in several colonies size was determined by using a spotting scope to count nests or adults; in several others photo transects were made from the airplane. In 1986 and 1987 estimates of the adult population were made using direct nest counts at small colonies; at larger colonies estimates were made by comparing aerial photographs to those made in earlier years; the largest colonies were estimated by Paul using knowledge from past experience of the colony and its size. In 1989 numbers were estimated from aerial surveys on most islands and by strip transects of mainland colonies. Ground counts were made by Paul and Jehl at the large colony at the Morton Salt Company and also on Gunnison Island. DWR also censused colonies at Utah Lake and Neponset Reservoir in 1982 and 1983. For details see Paul (1983, 1986, 1987, 1989).

The results (Table 1) show that in the 1980s gulls nested at 16–20 sites around the lake (Fig. 1), and that at some sites numbers varied from year to year. Most of the changes could be associated with a 10-foot fluctuation in lake levels, which caused the desertion of some colonies and the formation of others; the lake level rose from 4202′ in 1982 to 4211.8′ in 1987, and then receded to 4206.5′ in 1989.

For example, up to 18,000 gulls nested at Antelope Island in the mid–1960s, even though terrestrial predators (badger, fox, coyote) had access to the colony (Paul 1983 and personal observation). No gulls were present in 1982 (the first year of intensive surveys), perhaps because disturbance at a nearby excavation site discouraged nesting. Large numbers (nearly 33,000) returned in 1983, and

---

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TABLE 1. Numbers of breeding adult California Gulls at Great Salt Lake, Utah, 1982–1989[a]. Data from Utah Department of Wildlife Resources (Paul 1983, 1986, 1987, 1989).

Colony	1982	1983	1986	1987	1989	Remarks
Great Salt Lake						
1. Salt Creek WMA	200	50	50	100	ND[b]	Controlled population
2. Promontory Point	1172	0	0	0	0	Flooded 1983
3. Bear River Refuge	2492	4270	0	0	0	Flooded after 1983; controlled population
4. Perry Sewer Lagoon	0	0	1200	3165	35	Isolated after 1983, connected to mainland 1989
5. GSL Mineral	5356	0	0	NA	4500	Flooded 1983
6. Rocky Island	2037	976	20	20	300	Reduced in size by flooding in 1983, again 1986
7. Ogden Bay						
a. Pintail Flats	8706	2400	0	0	0	Flooded after 1983
b. Unit 1	0	2000	0	0	3592	Flooded after 1983
c. Unit 2	112	0	0	0	0	Flooded after 1982
d. Pasture	0	0	10,000	12,000+	0	Occupied as lake rose
8. Egg Island	3502	1170	0	0	0	Reduced in size in 1983; flooded 1984
9. White Rock	0	492	200	200	200	Area reduced 25% after 1983
10. Antelope Island	0	32,940	34,600	34,000	0	See text
11. Farmington Bay	20	250	0	0	0	Flooded after 1983
a. Turpin Dike	20	0	0	0	0	Flooded in 1983
b. Interior	0	250	0	0	0	Controlled population
12. Morton Salt Co.	9476	9660	9500	9500	43,025	Incorporated Antelope Island colony in 1989
13. Lake Point Salt Co.	2740	7072	0	0	0	Flooded after 1983
14. Hat Island	10,997	9507	9800	9800	12,000	Minor reduction in area
15. Gunnison Island	3032	9450	10,000	10,000	12,700	No change in habitat
16. Locomotive Springs	0	0	1100	225	200	
Subtotal GSL	49,862	80,487	76,470	79,010+	76,552	
Other colonies						
Geneva Steel, Utah Lake	6591	5982	ND	ND	ND	
White Lake	8981	7855	ND	ND	ND	
Neponset Reservoir	3680	4856	ND	ND	ND	
Subtotal others	19,252	18,693	[18,000]	[18,000]	[18,000]	
Grand total	69,114	99,180	94,470	97,010+	94,552	

[a] ± 15%

[b] no data

the colony remained fairly stable until 1989, when it was abandoned for unknown reasons. Concurrently, the Morton Salt colony, which had been stable at about 9500 birds from 1982–1988, increased to over 43,000, presumably by incorporating the Antelope Island birds.

At Ogden Bay, several shoreline nesting areas were inundated by rising water in 1982–83 (Paul, personal observation), causing the gulls to move inland in 1984 to a dike separating waterfowl management units. When the dike was inundated in 1985, the gulls moved farther inland and occupied a pasture (12,000 birds in 1987), which was accessible to mammalian predators. The pasture colony bred successfully through 1988 but was deserted in 1989 when the dike used in 1985 resurfaced and was reoccupied.

Rising water in the early 1980s also isolated the dikes at Perry Sewage Lagoons, allowing a colony to form there in 1984. The colony grew to over 3000 in 1987 and then was virtually abandoned (35 nests) in 1989, after its isolation was destroyed by the falling lake levels (Paul and Jehl, personal observation).

There are several other nesting locations in the vicinity of Great Salt Lake, of which three are at Utah Lake. The Rock Island colony, estimated at 2000 adults in 1932 (by Behle), grew to 27,850 adults in 1942 (Beck 1942). A subsequent rise in lake level in 1944 made the island largely unavailable. At that time a new site developed on a dike at the newly established Geneva Steel plant. Beck estimated its size at 6800 gulls in 1946. In 1979 the DWR estimated 12,320 pairs there; 1982 and 1983 counts were 6591 and 5924 adults, respectively. White Lake (a southern extension of Utah Lake) has been active since at least the 1960s. The DWR estimated 12,124 pairs in 1979; in 1982 and 1983 there were 8981 and 7855 breeding adults, respectively.

In Rich County, east of the Wasatch Range, gulls have nested at Neponset Reservoir since at least the 1960s. Counts in 1982 and 1983 were 3680 and 4856 adults.

The Utah Lake and Neponset Reservoir colonies are still active and currently hold approximately the same numbers as in the early 1980s (Paul, personal observation).

DISCUSSION

The California Gull is a highly adaptable species. Despite a 10-foot fluctuation in lake level, which led to major changes in the availability of breeding sites and in the size of individual colonies in the 1980s, the number of breeding adults at Great Salt Lake has remained essentially constant at about 75,000–80,000 birds through that decade and, apparently, since Behle's 1931 survey. This is surprising, in view of the major population increase this species has undergone in the twentieth century (Conover 1983) and an apparent increase in winter population at Great Salt Lake in recent years (Tove and Fischer 1988). The only apparent anomaly in the number of breeding birds is the drop in 1982, which evidently resulted from the temporary abandonment of Antelope Island. Estimating 18,000 birds at nearby colonies gives a total of ca. 93,000–98,000 breeding adults for the Great Salt Lake region.

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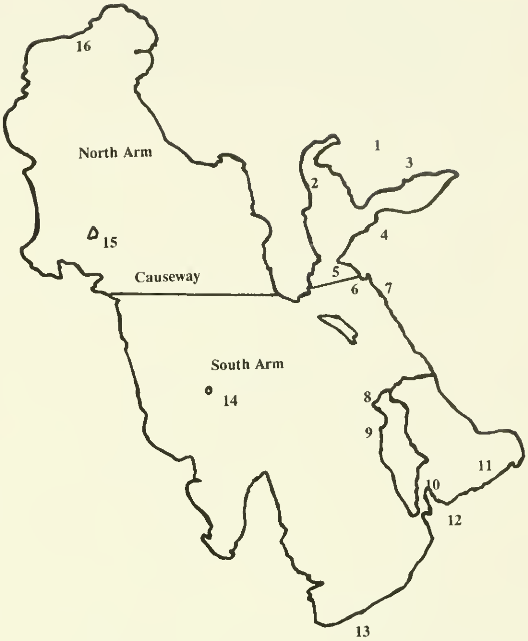

Fig. 1. Outline map of Salt Lake. Numbers refer to locations of California Gull colonies listed in Table 1.

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LONGITUDINAL DEVELOPMENT OF MACROINVERTEBRATE COMMUNITIES BELOW OLIGOTROPHIC LAKE OUTLETS

Christopher T. Robinson[1] and G. Wayne Minshall[1]

ABSTRACT.—Benthic macroinvertebrates were collected at several sites downstream of three oligotrophic lake outfalls in July 1986. Total numbers, biomass, and species richness increased rapidly immediately downstream from the outlets, and then either stabilized or continued to increase downstream in parallel with benthic organic matter standing crops. Filter feeder densities showed an initial buildup and then decline downstream from the outlets. Variability in longitudinal patterns of other functional feeding groups among lake outlets was related to differences in food quantity and quality, and microhabitat.

An additional set of samples was collected at Pettit Lake outlet in August 1986. Species richness and total density peaked sooner under baseflow conditions in August than under spring runoff conditions in June. Distributions of all functional feeding groups, except filter feeders, also differed between the two periods, reflecting differences in the physical environment. We conclude that reduced lentic inputs of particulate organic matter seston and improved habitat suitability downstream are responsible for the progressive development of macroinvertebrate communities in oligotrophic lake outlets. These data imply the importance of the habitat templet in the structuring of benthic communities.

Studies on the macroinvertebrate fauna in the outlet streams of meso- and eutrophic lakes have focused on the fate of lentic plankton or on longitudinal distribution of filter feeders in relation to progressively declining amounts of lake seston (Chandler 1937, Reif 1939, Cushing 1963, Maciolek and Tunzi 1968, Sheldon and Oswood 1977, Statzner 1978, Mackay and Waters 1986, Morin and Peters 1988). No comparable studies have been published for outlet streams of oligotrophic lakes. We hypothesized that streams draining oligotrophic mountain lakes would contain low levels of lake seston and that the invertebrate community would develop gradually as instream and adjacent riparian (allochthonous detritus) food sources developed. As a corollary, we expected that dense benthic filter feeder populations would not develop below the outlet or would dissipate rapidly as the limited seston resource was rapidly utilized. Our ultimate aim was to use the oligotrophic lake outlet invertebrate community as an analogue to low-head hydroelectric diversions to determine the distance required for recovery to prediversion community conditions under the "worst case scenario" of total elimination of invertebrate drift.

METHODS

Description of Study Sites

Studies were conducted during 8–15 June 1986 on three lake outlet streams located within the Stanley Basin of central Idaho (115°00′W longitude, 44°07′N latitude). Specifically, the streams drained Yellowbelly Lake, Stanley Lake, and Pettit Lake. Both the Yellowbelly Lake outlet stream and the Pettit Lake outlet stream flow into Alturas Lake

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Table 1. Physical measurements characterizing the three lake outlet streams at each transect for the preliminary lake outlet study (June 1986).

TRANS*	DIST (m)	%	W (m)	D (m)	V (cm/s)	SUB (cm^3)	LRIP (m)	RRIP (m)
Yellowbelly Lake outlet				Temp = 13 C				
1	10	1	10	.70	49	275	7	7
2	20	1	13	.67	58	186	7	7
3	40	1	15	.44	54	77	8	7
4	80	1	12	.49	97	333	8	6
5	160	1	8	.55	87	657	8	13
6	400	1	20	.45	63	50	5	15
Stanley Lake outlet				Temp = 10.2 C				
1	30	1	12	.86	72	109	10	2
2	220	1	10	.50	122	1691	20	15
3	240	1	8	.51	135	337	8	20
4	280	1	15	.59	110	229	5	15
5	360	1	13	.62	96	497	35	8
6	600	1	NA	.54	115	83	25	40
7	1000	1	18	.50	109	167	16	20
Pettit Lake outlet				Temp = 14.8 C				
1	10	1	15	.65	50	8	15	25
2	20	1	15	.51	55	3	15	50
3	40	1	15	.56	77	385	15	10
4	80	1	10	.62	90	299	2	15
5	160	1	15	.46	93	323	15	10
6	400	2	12	.44	137	358	10	12
7	900	2	14	.47	109	281	2	6

*TRANS = transect, DIST = distance downstream from lake outlet, % = percent gradient, W = stream width, D = mean stream depth, V = mean stream velocity, SUB = mean size of dominant substrate, LRIP = width of riparian zone on left side of stream, RRIP = width of riparian zone on right side of stream. N = 5 for D, V, and SUB for each transect.

Creek, which flows into the Salmon River. Stanley Lake Creek flows into Valley Creek before entering the Salmon River near the town of Stanley, Idaho. The three outlet streams were chosen because of their relatively pristine conditions and the large size of the lakes. Motor boat usage occurs on Pettit and Stanley lakes during summer. In addition, Pettit Lake has summer homes situated on the east side. Yellowbelly Lake is accessible primarily by foot.

Seven transects were located on each stream at geometrically increasing points downstream from the lake outlet (Table 1), but only six transects were placed at Yellowbelly Lake outlet because of a fish migration barrier located further downstream. The barrier altered the natural geomorphology of the stream by backing up and slowing streamflow for 100 m. Below the barrier the stream gradient greatly increased, thus again interfering with placement of transect 7. A fish migration barrier was located at Stanley Lake about 200 m downstream of the lake outlet. This barrier backed up streamflow to within 70 m of the lake. Here, transect 1 was placed 30 m downstream from the outlet and the remaining transects (2–7) starting 20 m below the barrier (about 220 m from the actual lake outlet, Table 1). Pettit Lake had a fish migration barrier located about 120 m downstream from the lake outlet. The barrier had no obvious effects on the natural streamflow; thus transect distances were left unmodified.

Physical measurements at each transect included percent gradient, stream width, mean stream depth, mean channel velocity, dominant substratum size, and width of the riparian zone on each side of the stream (Table 1). Temperature was recorded at midday for each stream. Generally, all three streams were similar in gradient (1–2%), stream width (10–15 m), stream depth (45–65 cm), mean stream velocity (70–120 cm/s), dominant substratum size (about 200 cm^3), and riparian width (about 15 m) (Table 1). Yellowbelly Lake outlet stream had relatively slower channel velocities, probably due to the migration barrier below transect 6. The effect of the barrier also is evident in the reduction of the

TABLE 2. Comparison of physical measurements in the Pettit Lake outlet stream at each transect for both June (J) and August (A) 1986. Distances, gradients, and riparian zone widths remained the same on both dates (see Table 1).

	W (m)		D (m)		V (cm/s)		SUB (cm^3)		Q (m^3/s)	
TRANS*	J	A	J	A	J	A	J	A	J	A
1	15	9	.65	.46	50	29	8	6	4.88	0.42
2	15	9	.51	.24	55	27	3	2	4.21	0.58
3	15	10	.56	.21	77	26	385	430	6.47	0.55
4	10	8	.62	.23	90	33	299	380	5.58	0.61
5	15	8	.46	.25	93	37	323	688	6.42	0.74
6	12	6	.44	.24	137	40	358	822	7.23	0.58
7	14	6	.47	.34	109	21	284	896	7.17	0.39

*TRANS = transect, W = stream width, D = mean stream depth, V = mean stream velocity, SUB = mean size of dominant substrate, Q = mean streamflow. N = 5 for each transect

dominant substrate size at transect 6 (Table 1). Stanley Lake outlet had a lower temperature than either Yellowbelly or Pettit Lake outlet streams (Table 1).

Pettit Lake outlet was chosen for a more extensive analysis in August 1986. The stream differed physically between the two study periods (Table 2). Mean stream width (by 4–5 m), mean stream depth (by 20–30 cm), mean channel velocity (by 30–100 cm/s), and mean streamflow (by 0.4–0.6 m^3/s) were lower in August than in June (Table 2). The dominant substratum size increased in August (by 12%–219%) except at transects 1 and 2, where the substratum was predominantly coarse sand (Table 2). This change in dominant particle size could be attributed to the restricted area for sampling during low flows.

Collection Methods

Five macroinvertebrate samples were collected at each transect using a modified Hess net (210 um mesh). Five additional benthic samples were collected from each transect at Pettit Lake outlet in August 1986. The circular net was placed firmly on the stream bottom, and a railroad spike was used to disturb the substratum within the net to a depth of 10 cm. Large cobbles were scrubbed by hand and removed for inspection of invertebrates. The contents of the net were collected, preserved in 10% formalin, and returned to the laboratory for analysis.

In the laboratory the invertebrates were hand-picked, identified, and enumerated using a dissecting microscope (8X). Chironomids were identified to family. Macroinvertebrate biomass (dry mass) was determined by drying the samples at 60 C and weighing. The remaining debris from each sample was used

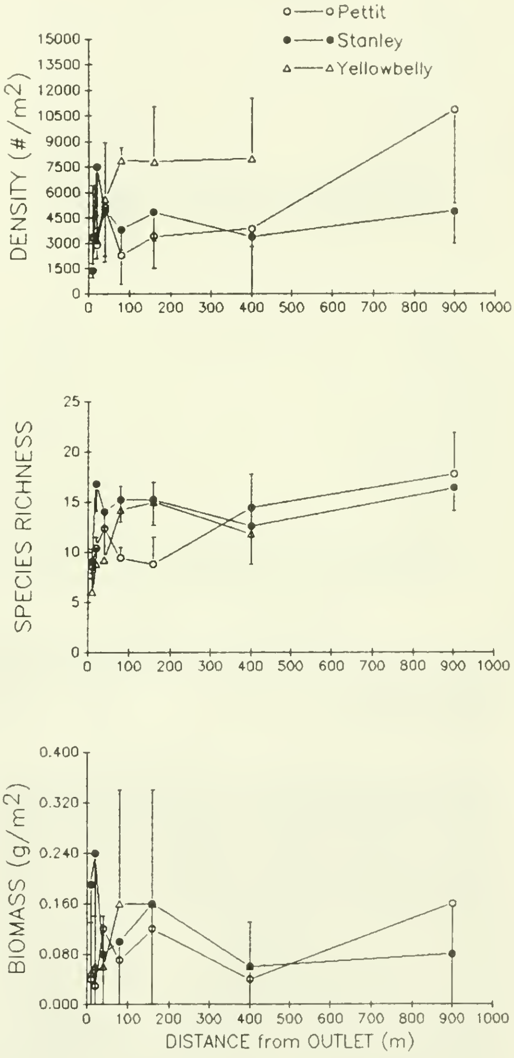

Fig. 1. Macroinvertebrate density, biomass, and species richness in three lake outlet streams in June 1986. Vertical bars indicate ± 1 standard deviation.

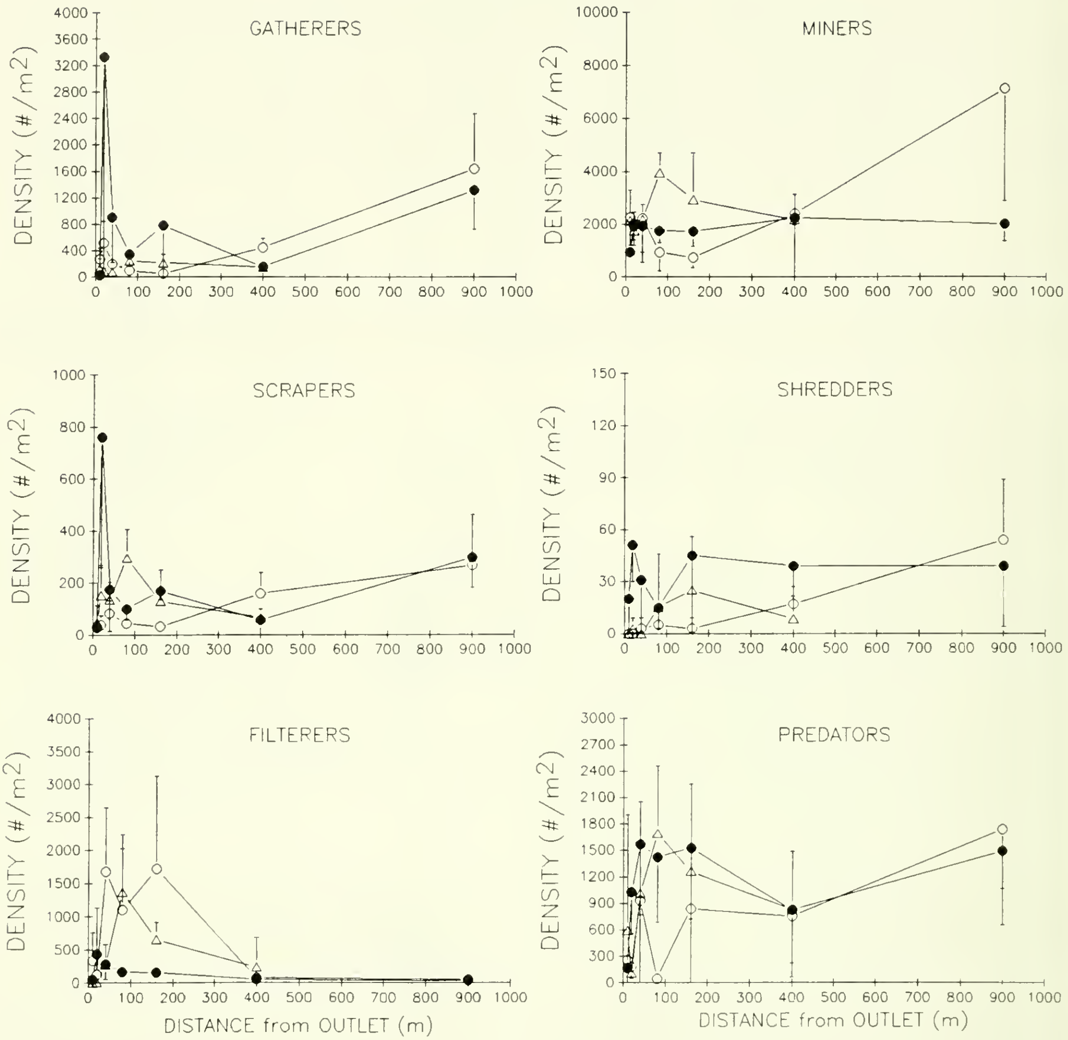

Fig. 2. Macroinvertebrate density by functional feeding group in three lake outlet streams in June 1986. Open circles = Pettit Lake, closed circles = Stanley Lake, and open triangles = Yellowbelly Lake. Bars represent ±1 standard deviation.

to determine the amount of benthic organic matter (AFDM). The sample was dried at 60 C, weighed, ashed at 550 C, rehydrated, redried at 60 C, and reweighed.

Results

Community Analysis

Macroinvertebrate density and biomass increased rapidly immediately below the outlets and then plateaued or, as in the case of Pettit and Stanley, decreased before stabilizing (Fig. 1). Total density and biomass at Stanley and Yellowbelly Lake outlets plateaued within 40 m. Yellowbelly Lake outlet had densities twice those of Pettit and Stanley Lake outlets, although biomass was similar among sites. This was probably in response to greater food availability as reflected in differences in organic matter standing crops between the two locations (Fig. 1). Macroinvertebrate density in Pettit Lake outlet was lower than that in the two other outlets at 80 m, but showed a relatively rapid increase to levels exceeding those of Stanley Lake outlet at transect 7.

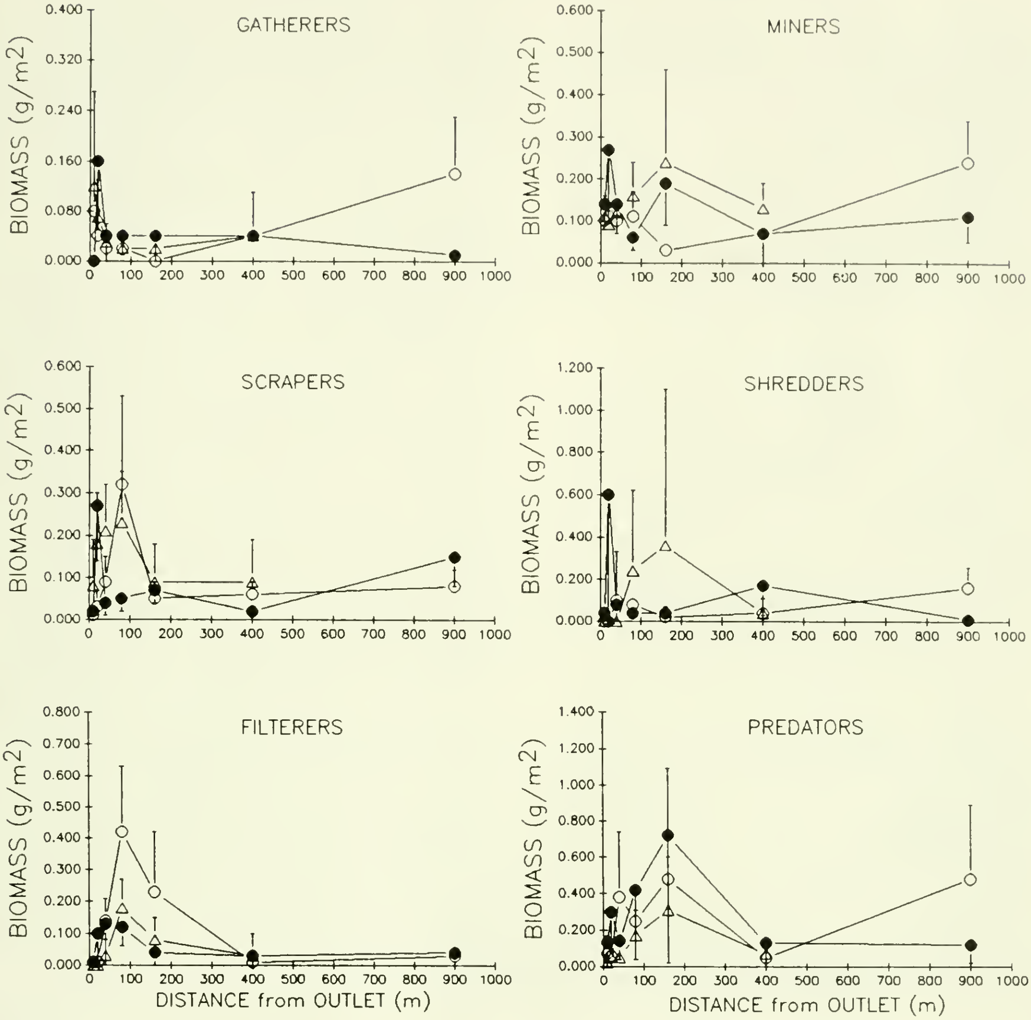

Fig. 3. Macroinvertebrate biomass by functional feeding group in three lake outlet streams in June 1986. Open circles = Pettit Lake, closed circles = Stanley Lake, and open triangles = Yellowbelly Lake. Bars represent ± 1 standard deviation.

Species richness increased immediately downstream from each lake outlet (Fig. 1). Pettit and Stanley Lake outlets showed slight declines in richness 20–80 m downstream, although there was a tendency, best seen at Pettit, to progressively add species with increasing distance from the lake.

Functional Feeding Group Analysis

STANLEY LAKE OUTLET.—The density and biomass of gatherers, scrapers, filterers, and predators each showed patterns comparable to that of total density and biomass (Figs. 2, 3). An exception was the extended high abundance of predators at 40–160 m. Shredder density downstream of 160 m showed a resurgence to high values observed at 20 m rather than a maintenance of values comparable to those found at 80 m as occurred for total density. Miners did not show the marked peak at 20 m seen for total numbers and for other functional feeding groups. Miners, such as chironomids, have been found to be abundant in lentic sediments, which may explain their lack of response immediately below lake outlets.

PETTIT LAKE OUTLET. — Gatherer, scraper, and miner density and biomass all showed

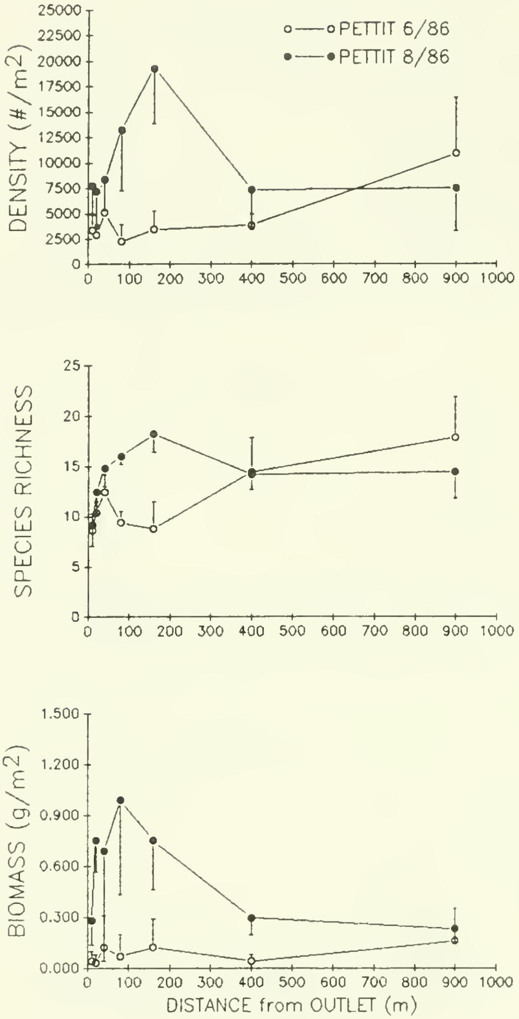

Fig. 4. Macroinvertebrate species richness, density, and biomass in Pettit Creek in June and August 1986. Bars represent ± 1 standard deviation.

patterns similar to those of total density and biomass. Filterer density and biomass peaked at 40 and 160 m (Figs. 2, 3). Predators showed an accentuated recovery in numbers at 160 m and continued high levels at 400 m in contrast to the pattern for total numbers. Predator biomass followed the pattern observed for filterer biomass (Fig. 3).

Yellowbelly Lake outlet.—The density and biomass of gatherers, filterers, and predators showed patterns similar to those of total density and biomass. However, the predator biomass deviated from the general trend by decreasing downstream of the 80-m transect (Figs. 2, 3). Filterer density and biomass peaked shortly below the outlet as was found at Pettit Lake outlet. The high filterer density and biomass were at a single location (80 m) rather than over an extended stretch (40–160 m) as at Pettit. Greater current velocity and substrate size may have facilitated colonization by filterers at 80 m at Yellowbelly Lake outlet (Table 1).

In general, the density and biomass of shredders followed the pattern seen for benthic organic matter at all three lakes. This was the "expected" pattern for all functional groups, based on the assumption of a lake outlet stream gradually accruing food downstream from allochthonous sources. Deviations from this pattern, especially by filter feeders, suggest "contamination" of the water by lake plankton. This was least evident at Stanley Lake outlet and most pronounced at Pettit Lake outlet. However, even at Pettit Lake outlet filter feeder populations declined rapidly within 160–400 m, indicating depletion of this material (Figs. 2, 3). Scraper density and biomass suggest that, for the most part, autochthonous sources of food were low, as would be expected for the headwater streams we were attempting to simulate. Yellowbelly Lake outlet at the 20-m transect is a notable exception. Although there were some minor deviations, data for density and biomass of functional feeding groups showed similar patterns (Figs. 2, 3).

Seasonal Study of Pettit Lake Outlet

Longitudinal patterns of total density, biomass, and species richness were somewhat different in August from those found in June (Fig. 4). Animal density, biomass, and species richness peaked sooner in August than in June and were not significantly different downstream of the 400 m transect. Total density and biomass increased downstream to 160 m, declined markedly for the next 240 m, and then stabilized in August (Fig. 3). The peak in abundance 40–200 m downstream of the lake outlets in August suggests greater production occurring at this time of year, possibly due to increases in stream temperature, solar radiation, and lentic inputs.

Longitudinal distributions of all functional feeding groups except filterers and scrapers differed in August from those in June (Figs. 5, 6). Filterer density and biomass peaked early

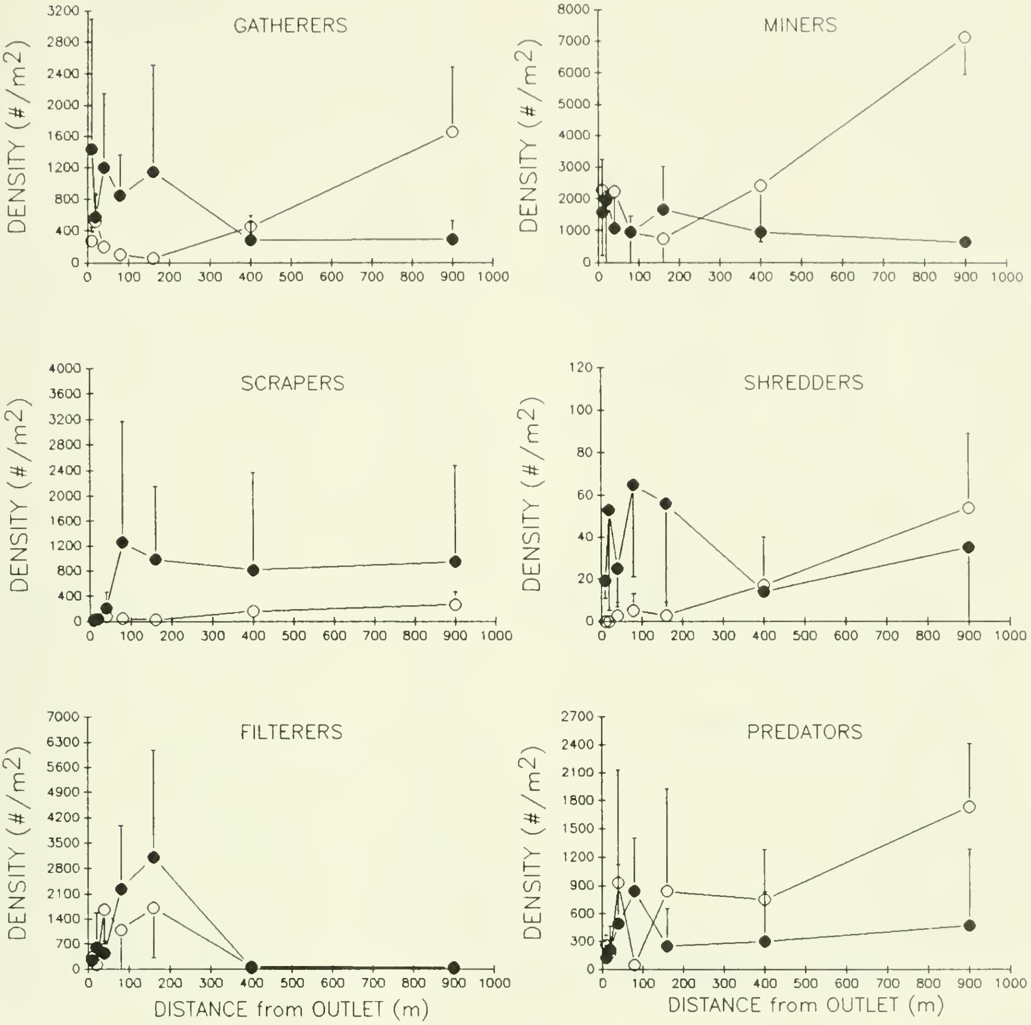

Fig. 5. Macroinvertebrate density by functional feeding group in Pettit Lake outlet in June and August 1986. Open circles = June, closed circles = August. Bars represent ±1 standard deviation.

and then virtually disappeared from the community downstream for both sampling dates. Gatherers, miners, and shredders increased in abundance (density and biomass) downstream of the outlet in June, whereas gatherers, miners, and shredders had high densities through 160 m and then decreased to low values at 400 and 900 m in August. Gatherer, miner, and shredder biomass was similar among transects in August. Scrapers peaked in biomass at 80 m in June but displayed similar biomass values among transects in August (Fig. 6). The main difference in predator abundance between the two dates was the reduced peak at 40 m and the decrease at 80 m in June that was absent in August (Figs. 5, 6).

DISCUSSION

The results support our hypothesis of a gradually developing stream community (greater numbers/m^2 and taxonomic complexity) with progressive distance downstream of a lake outlet. The distance required for the development of full community potential (i.e., the recovery distance following complete interception of incoming drift) could not be determined precisely and seems to vary

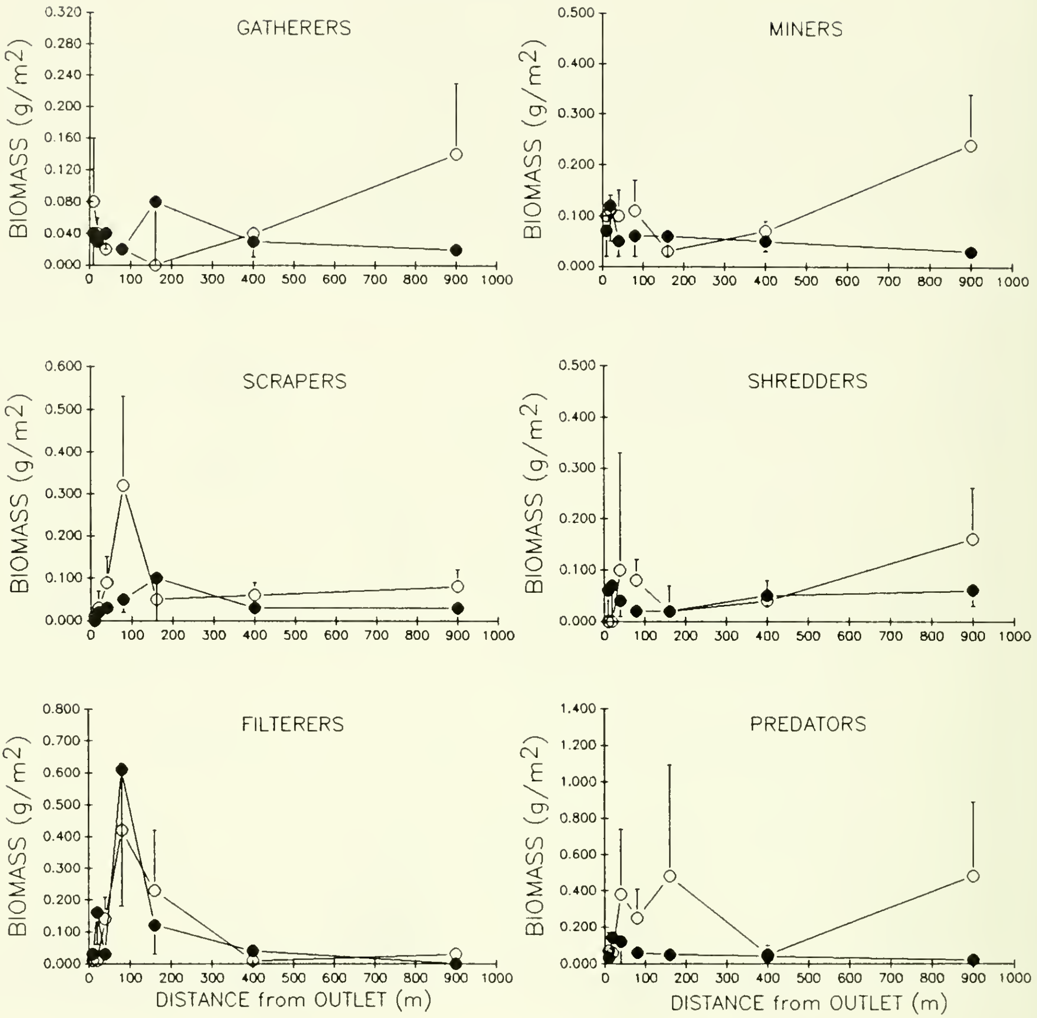

Fig. 6. Macroinvertebrate biomass by functional feeding group in Pettit Lake outlet in June and August 1986. Open circles = June, closed circles = August. Bars represent ± 1 standard deviation.

widely depending on the particular stream and time of year. In June, during a period of relatively high discharge, "recovery," measured in terms of species richness and total density, ranged from 20 m at Stanley Lake to over 900 m at Pettit Lake. During near base flow conditions in August, community development in Pettit Lake seemed to be much more rapid than in June, peaking somewhere between 160 and 400 m. These data suggest that community development is impeded under conditions of high flow. Additional measurements should be made in several outlet streams having unaltered flows and channels so that the full distances required for recovery during each season and the factors responsible for the different rates of community development among streams can be established.

Our results also show a restricted distribution by filter feeders. The decline from peak numbers below the outlet was more rapid than reported by Sheldon and Oswood (1977), thus supporting our prediction that oligotrophic lakes will show more limited supplies of seston and consequently a more restricted distribution of filter feeders in their outlet streams than meso- or eutrophic lakes. In addition, we found that filter feeder abundances increased from low numbers immediately below the outlet to peak numbers some distance (40–80 m) downstream. This differs from the progressive downstream decrease in filter feeder abundance modeled by Sheldon and Oswood (1977) and may have been overlooked by them because they sampled no closer than 25 m below the lake outlet. A parabolic relationship of filterer density with distance rather than a negative linear regression may be due to suboptimal environmental (e.g., velocity) or biotic conditions near the outlet. Current velocities in Pettit Creek were less near the outlet (26–29 cm/s) than further downstream (33–40 cm/s) and may not have met the needs of filterers for feeding or respiration. Further, changes in substratum characteristics occurred within 40 m of the lake outlet (Table 1). Mackay and Waters (1986) suggest that changes in filterer abundances between the impoundments they studied may be due to a greater abundance of attachment sites.

Our data contribute a spatial dimension to the recolonization of stream benthos by macroinvertebrates. These data suggest the importance of the habitat templet in the structuring of benthic communities. This implies faster recovery or community development in streams below lake outlets in which adequate structural habitat is present. These data suggest that low-head hydro installations can impact macroinvertebrate communities by reducing the structural attributes of the habitat templet.

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SPATIAL PATTERN AND INTERFERENCE IN PIÑON-JUNIPER WOODLANDS OF NORTHWEST COLORADO

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ABSTRACT.—The local spatial arrangement of the coniferous trees *Pinus edulis* and *Juniperus osteosperma* was mapped in two woodland stands and measured in two shrub-dominated stands in the semiarid Piceance Basin of northwest Colorado. In the woodlands, small trees were often clumped, while medium and large trees were either randomly or uniformly dispersed. Significant regressions were obtained between a tree's basal area or canopy area and the area of its Dirichlet domain (the region closer to it than to any other tree). Both findings from the woodland stands accord with results obtained by other workers in other vegetation. Like earlier workers, we interpret these patterns to indicate density-dependent mortality and density-dependent depression of growth rates among the trees in the woodlands. In contrast, the trees in the shrub-dominated stands are located at random with respect to each other. However, they are strongly associated with shrub cover. Apparently, tree seeds arrive in these stands primarily by long-distance dispersal, and the establishment of seedlings is more likely in the shade of shrubs.

Since plants are sessile and their growth is plastic, their arrangement in space and their sizes can reflect the history of their interactions with each other and with the environment. With long-lived, slow-growing plants, studying pattern may be the only feasible way to discover which processes and interactions are important in determining community structure.

We used some of the methods compared by Goodall and West (1979) to study the local spatial arrangement (pattern) of the small coniferous trees *Pinus edulis* and *Juniperus osteosperma* in four stands in the semiarid Piceance Basin of northwest Colorado. Our goals were twofold. First, we wished to determine whether the differences between methods Goodall and West (1979) detected in artificial populations are borne out in more complex real populations. Second, we wished to infer the processes that influence the establishment of seedlings and the growth and mortality of plants.

STUDY AREA

The Piceance Basin occupies about 3000 km^2 in Garfield and Rio Blanco counties of northwest Colorado. Elevations range from 1707 to 2743 m (Tiedeman and Terwilliger 1978). The climate is semiarid with average annual precipitation ranging from 28 cm in the northwest to 63.5 cm in the southeast. About half of the annual total falls as snow and most of the remainder as rain in late-summer thunderstorms. In the short term, precipitation is unpredictable and variable (Wymore 1974).

The average annual temperature is 7 C at 1825 m (the elevation of the only permanent weather station in the basin), with a minimum monthly average in January of −5.9 C and a maximum monthly average in July of 20.3 C. The average annual temperature decreases by approximately 0.85 C for every 100 m increase in elevation. Both temperature and precipitation are strongly influenced by local topography (Wymore 1974).

We studied the spatial patterns of *Pinus edulis* Engelm. and *Juniperus osteosperma* (Torr.) Little (piñon and Utah juniper). Nomenclature follows Goodrich and Neese (1986). *P. edulis* and *J. osteosperma* are small coniferous trees common throughout the western United States, where they form mixed stands, often with an understory of scattered grasses, forbs, and shrubs. They commonly attain heights of 6–8 m, and both reproduce by seed. *P. edulis* usually possesses a single stem, while *J. osteosperma* is often multistemmed.

The vegetation of the basin includes shrublands and woodlands of various floristic compositions. Piñon-juniper woodlands (as described in Tiedeman and Terwilliger 1978) have open canopies dominated by *P. edulis* and *J. osteosperma* and occur on broad, flat ridge tops at elevations between 1890 m and 2170 m, where soils are shallow, rocky, light brown, sandy loams (Entisols). Shrublands dominated by *Artemisia tridentata* Nutt. (sagebrush flats) often occur on the same ridges as do piñon-juniper woodlands, at roughly the same elevations, but where soils are finer and deeper. Where piñon-juniper woodlands abut sagebrush flats, zones of intermediate vegetation are often found. In these intermediate areas, the vegetation is dominated by *Artemisia*, with small, scattered individuals of *P. edulis* and *J. osteosperma*. Few of the trees overtop the shrubs.

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We studied two piñon-juniper woodlands (stands A and B), which were dominated by mature *P. edulis* and *J. osteosperma*, with little shrub understory. The canopies in these stands are not closed, but individual canopies sometimes abut or overlap. It is known from others (Fowells 1965) and from personal observation that the roots of these trees usually extend beyond the canopy. Thus, neighboring trees which do not seem to be competing for light may nonetheless be competing belowground for water or nutrients. These stands lie at elevations of 2164 m and 1890 m, which approximate the elevational limits of this vegetation in the basin. Stand A slopes 1.5° and faces to the northwest (N62°W). Stand B slopes 3.0°, facing to the north-northwest (N22°W).

Stands C and D are intermediate between piñon-juniper woodlands and sagebrush flats. None of the trees in these stands is as large as the largest trees in the piñon-juniper woodlands, although many bear cones and are thus sexually mature. These stands occupy ridge tops at elevations of 2164 m and 1981 m. Stand C slopes 4.5°, facing west (N80°W), and stand D slopes 6.5°, facing north (N5°W).

METHODS

Goodall and West (1979) reviewed pattern methods based on analyses of artificial populations. They compared the statistical powers of the methods, that is, the probabilities of rejecting a false null hypothesis. With large samples, all the tested methods gave results reflecting the true dispersion pattern of artificial populations, with powers approaching 100%. With smaller samples, however, methods differed in power. We used those having the greatest power with small samples: the variance/mean ratio (Clapham 1936) among quadrat methods, and the indices of Hopkins (1954) and Pielou (1959, 1960, 1961) among distance methods (see descriptions below). We also compared the frequencies of quadrats containing exactly 0, 1, 2, . . . plants with the expected Poisson distribution by a chi-squared goodness-of-fit test.

In addition to these methods, we included a measure of pattern that uses information not only about the locations of plants but also about their sizes. The Dirichlet domain (or Thiessen or Voronoi polygon) of a plant comprises all the points closer to that plant than to any other (Honda 1978, Jack 1967, Mead 1971, Mithen, Harper, and Weiner 1984). Its size thus represents the area more easily accessible to the plant than to its neighbors and may represent the amount of resources captured or sequestered by a plant, or potentially more available to it than to its neighbors. This in turn may influence the plant's growth and fitness and indicate what effect, if any, its neighbors have on it. To detect whether this is the case, we regressed the areas of plants' Dirichlet domains on the sizes of the plants.

The variance/mean ratio test (Clapham 1936) is based on the expectation that, in a randomly dispersed population, the frequency distribution of quadrats containing exactly 0, 1, 2, 3, . . . individuals approximates the Poisson distribution. One property of this distribution is that its mean and variance are equal, and their ratio therefore unity. The distribution of this ratio in large samples is approximately normal, with a mean of 1 and a standard deviation of $(2/n-1)^{1/2}$ (Goodall and West 1979), where n is the sample size (number of quadrats). In regularly dispersed populations the ratio is less than 1, in aggregated ones greater.

Hopkins's (1954) index A is based on the expectation that, in a randomly dispersed population, the average distance from randomly located points to the nearest plant equals the average distance between plants and their nearest neighbors. Hopkins proposed the ratio of these two averages as his index:

$$A = (\Sigma P_i^2)/(\Sigma I_i^2)$$

where P_i and I_i are the sums of equal numbers of distances from random points to the nearest plant and from randomly selected plants to their nearest neighbors, respectively. In a randomly dispersed population, the expected value of A is 1, and for large samples its frequency distribution is approximately normal. Values of A larger than 1 indicate aggregation, less than 1 regularity.

Pielou (1959, 1960, 1961) developed two distance methods to measure pattern. The first uses a sample of distances from randomly located points to the nearest plant and an independent estimate of plant density. From these a statistic, alpha_p, can be calculated as follows:

$$\text{alpha}_p = \text{pi(D)omega}_p$$

where D is the density of the plants, omega_p is the mean squared point-to-plant distance, and pi is the trigonometric constant.

The second method (Pielou 1960) uses a sample of distances from randomly chosen plants to their nearest neighbors. A statistic alpha_i is calculated in the same way as alpha_p, substituting the mean squared plant-to-plant distance for the mean squared point-to-point distance. Pielou (1959) provides tables of confidence intervals and significance levels for values of alpha_i and shows how they may be used to interpret alpha_p (Pielou 1960).

We mapped the location of each *Pinus edulis* and *Juniperus osteosperma* 10 cm tall or taller in parts of stands A and B. The mapped area in stand A was 2250 m^2; in stand B it was 2500 m^2. We checked the accuracy of the maps by comparing plant-to-plant distances calculated from map coordinates to the same distances measured in the field. The greatest difference was about 10 cm.

We classified plants into three height-classes. Small plants were 10 cm to 1 m tall, medium plants between 1 m and 3 m tall, and tall plants were taller than 3 m. The tallest trees in our stands were about 5 m tall. Small plants were not mapped in about one-third of stand A.

For each *P. edulis* in these stands we measured one canopy diameter in an arbitrary direction and estimated the area of its canopy as if it were circular. The living canopies of *J. osteosperma* were often interrupted by dead branches. We measured the living portions of their canopies and summed the areas estimated from these. Basal areas were calculated for both species from stem diameters measured at ground level. For multistemmed plants, the basal areas of all living stems were summed.

We measured the dispersion patterns of the plants on these maps, using both quadrat and distance methods. Small plants were sampled with quadrats 2.5 m on a side (in map scale), medium and tall plants with quadrats 5 m on a side. Quadrats were placed at the intersections of a regular grid of lines 5 scale-meters apart; thus every point on the map was included in exactly one quadrat of a given size. There were 100 large and 400 small quadrats in stand B. Stand A was more irregular, encompassing 90 large and 230 small quadrats.

The spatial dispersions of each size class and species were measured separately and pooled. That is, the null hypothesis of random spatial dispersion was tested by five indices for small *P. edulis*, small *J. osteosperma*, all small plants, medium *P. edulis*, medium *J. osteosperma*, all medium plants, tall *P. edulis*, tall *J. osteosperma*, all tall plants, medium and tall *P. edulis* combined, medium and tall *J. osteosperma* combined, and all medium and tall plants combined.

We constructed Dirichlet domains (Honda 1978, Jack 1967, Mead 1971, Mithen, Harper, and Weiner 1984) for the plants by drawing lines connecting each plant to its immediate neighbors, and then constructing perpendicular bisectors of these lines (Fig. 1). Note that we did not weight the distance from a plant to the bisector by the size of the plant, and thus there is no necessary correlation between the size of a plant and the size of its Dirichlet domain. We estimated the areas of the Dirichlet domains by cutting the polygons from the maps and weighing them. We regressed the areas of the Dirichlet domains on the basal areas, and separately on the canopy areas, of their plants. Regressions on basal areas were compared to regressions on canopy areas, with and without logarithmic transformation, by graphical analysis of residuals.

In stands C and D we located every *P. edulis* and *J. osteosperma* 10 cm or more in height within a square 50 m on a side, noting whether it had become established under a plant canopy or in the open, based on observations of each

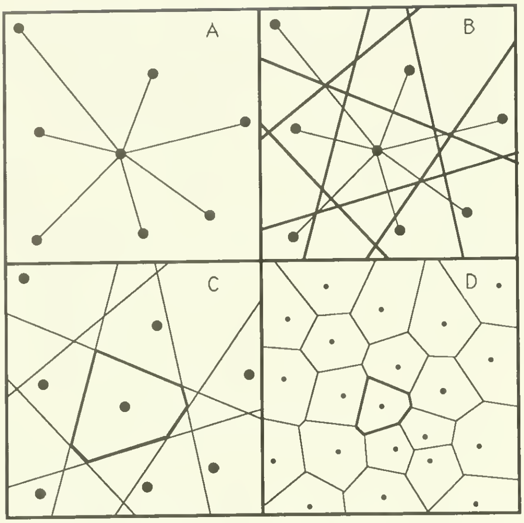

Fig. 1. Construction of Dirichlet domains.

a. Draw line segments connecting a focal plant to its neighbors.

b. Draw the perpendicular bisector of each line segment.

c. The Dirichlet domain is the region closer to the focal plant than all the perpendicular bisectors.

d. Repeat for each plant. The Dirichlet domain of each plant is the region closer to it than to any other plant.

tree's association with living or dead shrubs. We measured total plant cover of all species with two 50-m line intercepts. The association of *P. edulis* and *J. osteosperma* with plant cover was tested by a chi-squared test. We did not map these stands but measured distances between neighboring trees in the field. We used Pielou's alpha$_1$ to describe the spatial dispersion of the two tree species.

RESULTS

Table 1 shows the number of *P. edulis* and *J. osteosperma* in each stand and the corresponding numbers per hectare. Table 2 shows the five dispersion indices for the trees in stands A and B, and Table 3 the interpretations of these values. In the woodland stands (A and B) small plants tend to be clumped, and larger plants tend to be randomly or uniformly dispersed. The sequence from clumped to random to uniform is violated in only three instances (asterisks in Table 3). These violations may be the result of chance, since the tests for significance were all set at the 5% level and some spurious results are expected among such a large number of separate tests.

All log-log transformed regressions of Dirichlet domain areas on plant canopy areas and basal areas in stands A and B are significant at the 5% level, except for that of *J. osteosperma* in stand A (Table 4, Fig. 2). These regressions show that, on average, larger plants have larger Dirichlet domains and are correspondingly farther from their neighbors. The Dirichlet domains of small plants are more variable in area than those of larger plants. Logarithmic transformation of both variates improves the distribution of variates and residuals and produces reasonable conformity with the assumptions of regression, but it does not change the significance of the regressions. These results are similar to those of regressing the distance between a pair of neighboring plants on the sum of their sizes (Welden 1984, Welden, Slauson, and Ward 1988, cf. Fuentes and Gutierrez 1981, Gutierrez and Fuentes 1979, Nobel 1981, Phillips and MacMahon 1981, Pielou 1960,

TABLE 1. Stand censuses, divided by height categories (10 cm ≤ small < 1 m ≤ medium < 3 m ≤ tall) and by species. In parentheses are numbers per hectare.

		Small plants	Medium plants	Tall plants	Total
Stand A	*Pinus edulis*	61 (432)	56 (229)	67 (274)	184 (753)
	Juniperus osteosperma	26 (184)	12 (49)	39 (160)	77 (315)
Stand B	*P. edulis*	88 (352)	32 (128)	11 (44)	131 (524)
	J. osteosperma	86 (344)	9 (36)	41 (164)	136 (544)
Stand C	*P. edulis*	56 (224)	22 (88)	1 (4)	79 (316)
	J. osteosperma	7 (28)	7 (28)	0	14 (56)
Stand D	*P. edulis*	47 (188)	30 (120)	4 (16)	81 (324)
	J. osteosperma	34 (136)	46 (184)	17 (68)	97 (388)

TABLE 2. Values of dispersion indices in stands A and B. Indices are identified in the text and these values are interpreted in Table 4. A dash indicates that the test could not be performed.

Stand	Distance methods						Quadrat methods			
	alpha$_p$		alpha$_i$		A		chi^2		var/mean	
	A	B	A	B	A	B	A	B	A	B
P. edulis										
Small	0.93	1.04	1.12	0.84	0.83	1.21	12.2	25.0	1.27	1.98
Medium	0.98	1.23	1.15	0.66	0.85	1.83	5.97	—	1.72	1.60
Medium and tall	1.00	0.74	1.04	0.97	0.96	1.38	2.90	2.16	1.48	1.28
Tall	0.84	0.38	0.88	0.91	0.95	0.42	0.17	—	1.10	0.89
J. osteosperma										
Small	1.03	1.36	1.04	1.07	0.99	1.27	—	29.4	1.52	1.15
Medium	0.61	1.06	0.84	0.64	0.72	1.65	—	—	1.04	0.86
Medium and tall	0.73	0.93	1.09	1.29	0.78	0.73	0.24	2.12	0.96	0.86
Tall	0.73	0.73	1.18	1.39	0.75	0.54	0.24	1.10	0.97	0.82
Species combined										
Small	1.25	1.29	0.79	0.86	1.58	1.50	18.1	8.18	1.62	1.65
Medium	1.17	1.58	0.96	0.54	1.22	2.94	2.28	10.9	1.44	2.22
Medium and tall	1.06	0.86	0.94	1.14	1.12	0.92	4.35	0.91	1.34	1.19
Tall	0.92	0.74	0.98	1.13	0.78	0.59	0.60	3.76	1.04	0.95

TABLE 3. Pattern analyses of stands A and B. C indicates that the plants are clumped, R that they are randomly dispersed, U that they are uniformly dispersed. All indicated nonrandom dispersions are significant at the 5% level. A dash indicates that the test could not be performed. Asterisks denote contradictions to the general trend of C – R – U with increasing plant size.

Stand	Distance methods						Quadrat methods			
	alpha$_p$		alpha$_i$		A		chi^2		var/mean	
	A	B	A	B	A	B	A	B	A	B
P. edulis										
Small	R	R	R	R*	R	R*	C	C	C	C
Medium	R	R	R	C	R	C	C	—	C	C
Medium and tall	R	U	R	R	R	R	R	R	C	R
Tall	R	U	R	R	R	R	R	—	R	R
J. osteosperma										
Small	R	C	R	R	R	R	—	C	C	C
Medium	U	R	R	R	R	R	—	—	R	C
Medium and tall	U	R	R	R	R	R	R	R	R	R
Tall	U	U	R	U	R	U	R	R	R	R
Species combined										
Small	C	C	R	R*	R	C	C	C	C	C
Medium	R	C	R	C	R	C	R	C	C	C
Medium and tall	R	R	R	R	R	R	R	R	C	R
Tall	R	U	R	R	R	U	R	R	R	R

1961, Yeaton and Cody 1976, and Yeaton, Travis, and Gilinsky 1977).

Plant cover (primarily of *Artemisia*) in stand C was approximately 20%, and about 96% of the *P. edulis* and about 71% of the *J. osteosperma* had become established under plant canopy. Plant cover in stand D was about 18%, and about 93% of the *P. edulis* and about 87% of the *J. osteosperma* had become established under plant canopy. The probability that establishment of *P. edulis* or *J. osteosperma* is random with respect to plant cover is less than .001 in every case. The pattern statistic alpha$_i$ (Pielou 1960) showed no significant deviations from random dispersion among *P. edulis* or *J. osteosperma* in stands C and D.

DISCUSSION

Pielou (1959) and Goodall and West (1979) show that distance methods are more sensitive to uniformity and quadrat methods are

Table 4. Coefficients of log-log transformed regressions of Dirichlet domain area on canopy and basal areas. Significance is the probability of such data if the true slope and r equal zero.

Species	Stand	n	r^2	Y-intercept	Slope	Significance
P. edulis						
Independent variable						
ln (canopy area)	A	98	0.056	10.12	0.13	0.019
ln (basal area)			0.052	11.05	0.11	0.024
ln (canopy area)	B	33	0.272	5.15	0.26	0.002
ln (basal area)			0.191	6.81	0.21	0.011
J. osteosperma						
ln (canopy area)	A	27	0.031	12.50	−0.06	0.377
ln (basal area)			0.020	12.04	−0.04	0.479
ln (canopy area)	B	31	0.367	5.41	0.23	0.000
ln (basal area)			0.352	6.84	0.18	0.000
Species combined						
ln (canopy area)	A	125	0.039	10.49	0.10	0.027
ln (basal area)			0.047	11.15	0.09	0.015
ln (canopy area)	B	64	0.333	5.27	0.25	0.000
ln (basal area)			0.268	6.88	0.18	0.000

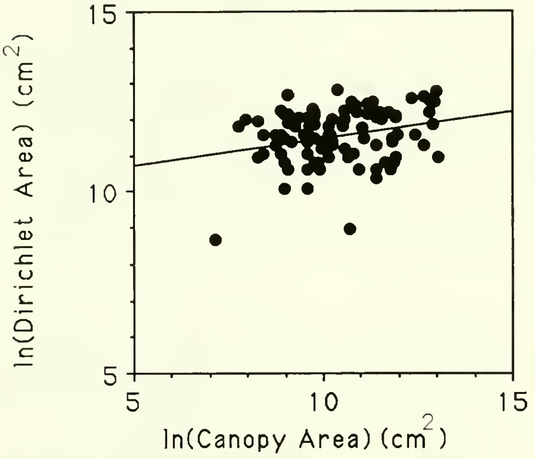

Fig. 2. Regression of Dirichlet domain area on canopy area of piñons in stand A. Both variates have been transformed to their natural logarithms.

more sensitive to clumping. This is borne out by Table 4, where it can be seen that the quadrat methods never detected uniform dispersion while the distance methods did. The distance methods, on the other hand, failed to detect clumping in several cases where it was detected by the quadrat methods.

The trees in the woodland stands (A and B) appear to be interfering (*sensu* Harper 1961, 1977) with one another, either by competition or by allelopathy. The trend from clumped to random to uniform dispersion with increasing plant size suggests density-dependent mortality. Density-independent mortality in a clumped population might conceivably reduce sample sizes in successively larger size-classes until the clumping is no longer detectably different from a random dispersion, but it seems unlikely that it could produce a uniform dispersion (Phillips and MacMahon 1981).

The significant regressions of Dirichlet domain area on plant size indicate density-dependent mortality or density-dependent suppression of growth, or both. We envision two processes leading to this result. First, plants that become established farther from preexisting neighbors become larger because they have access to more unexploited (or unsequestered) resources. Second, established plants prevent the establishment of new neighbors nearby, or impede their growth, because they have exploited (or sequestered) most of the resources in their neighborhoods.

Mithen, Harper, and Weiner (1984) found significant positive relationships between Dirichlet domain area and plant dry weight in even-aged greenhouse populations of *Lapsana communis* L. Although the conditions of their experiments are different (particularly since their plants germinated synchronously), their interpretations of their results are similar to ours here.

Pielou's (1959, 1960) method did not detect any deviation from random spatial arrangement in stands C and D. However, both tree species are significantly associated with plant cover. We presume that these trees became established after long-distance dispersal (> 100 m) from nearby woodlands. The significant interaction in these stands is evidently not interference between neighboring trees, but amelioration of abiotic stress under the canopies of preexisting plants. Fowells (1965) reports that *P. edulis* requires shade early in its development.

Our evidence for these interpretations is circumstantial. However, given the long lives and slow growth of these plants, and the varying physical environment of the study area, such evidence may be the most informative. These pattern methods integrate the effects of environment and biotic interactions over the life spans of the plants, a time scale not usually accessible to more mechanistic methods.

All our inferences of processes leading to the present pattern require further examination. Although *J. osteosperma* has been reported to produce allelochemicals (Jameson 1971), experiments should be done to determine whether allelopathic effects occur under the conditions and in the soils of the Piceance Basin, and more field studies are needed to determine whether establishment occurs more often near neighbors or far from them. The dynamic behavior of the various pattern indices and regressions should be explored under conditions of density-dependent and density-independent mortality.

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TRAMPLING DISTURBANCE AND RECOVERY OF CRYPTOGAMIC SOIL CRUSTS IN GRAND CANYON NATIONAL PARK

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ABSTRACT.—Cryptogamic soil crusts in Grand Canyon National Park were trampled by hikers, under controlled conditions, to determine how rapidly they were pulverized and how rapidly they recovered. Only 15 trampling passes were required to destroy the structure of the crusts; visual evidence of bacteria and cryptogam cover was reduced to near zero after 50 passes. Soil crusts redeveloped in just one to three years, and after five years the extensive bacteria and cryptogam cover left little visual evidence of disturbance. Surface irregularity remained low after five years, however, suggesting that recovery was incomplete.

Cryptogamic soil crusts are common and functionally significant features of arid ecosystems. Bacteria, algae, fungi, lichens, and mosses bind surface soil particles together, creating a highly irregular surface crust of raised pedestals (typically black and several cm tall) and intervening cracks. Crusts provide favorable sites for the germination of vascular plants (St. Clair et al. 1984) and play important roles in water conservation (Brotherson and Rushforth 1983) and nitrogen fixation (Snyder and Wullstein 1973). These crusts are particularly significant in reducing soil erosion. Soil aggregation raises the wind and water velocities required to detach soil particles, while the irregular soil surface tends to reduce wind and soil velocities (Brotherson and Rushforth 1983). Increased water infiltration in crusted soils also reduces runoff and erosion. Increased soil stability is highly significant in arid environments where sparse vegetation and surface soil organic matter as well as sporadic torrential rainfall contribute to a high erosion hazard.

A number of recent studies have examined the response of cryptogamic soil crusts to disturbance by grazing and by fire (Anderson et al. 1982, Johansen et al. 1984, Johansen and St. Clair 1986, Marble and Harper 1989). The results of these studies suggest that crusts are unusually fragile and can be seriously disrupted by low levels of disturbance that have no noticeable effect on vascular plants (Kleiner and Harper 1972).

The fragility of crusts presents unique challenges to land managers attempting to avoid adverse impacts on desert lands. This is particularly true in the many national parks located in the arid lands of the southwestern United States. The popularity of these desert parks has made it increasingly difficult for managers to meet management objectives that stress the maintenance of natural conditions and processes. Many hikers now visit places that a decade or two ago had few visitors. These backcountry users can significantly impact cryptogamic soil crusts if they wander off the trail or set up camp in crusted areas.

The purpose of this study was to examine the effect of trampling disturbance on soil crusts to better understand how rapidly they are disturbed and how quickly they can recover. It was conducted in the backcountry of Grand Canyon National Park on a study site located close to the Bass Trail, at an elevation of about 1,650 m. The site is flat, and during the study the soil crusts exhibited well-developed pinnacles and were conspicuously blackened with lichens. The vegetation type is a *Coleogyne ramosissima–Pinus edulis–Juniperus osteosperma* woodland (Warren et al. 1982). Soils, derived from sandstones of the Supai Group, are shallow and highly sandy. The climate can be characterized as that of a cold desert; annual precipitation is about 25 cm with a bimodal occurrence in winter and summer.

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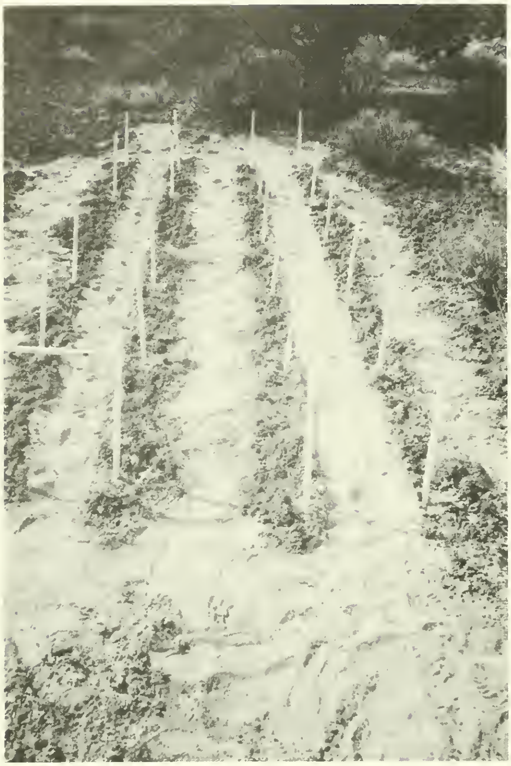

Fig. 1. The two trampling lanes immediately after 50 passes in tennis shoes (left) and 250 passes in lug-soled boots (right). Note horizontal bar for measuring vertical distances.

METHODS

Two lanes about 6 m long and 0.4 m wide were delineated with lengths of PVC pipe in an area of well-developed, undisturbed soil crust (Fig. 1). The lanes were separated by a path that was trampled during the period when the treatments were applied and then allowed to recover afterward. One lane was trampled by a 75-kg person in tennis shoes, the other by an 86-kg person in lug-soled boots. Measurements were taken prior to trampling and after 5, 15, 25, and 50 passes, a pass being one walk down the lane at a normal gait. The lane trampled with lug-soled boots was trampled another 200 times, for a total of 250 passes. Subsequent measurements were taken one, three, and five years after the treatments were administered. Treatments and measurements occurred in late spring—April or May 1984.

TABLE 1. Changes in the cryptogam cover, vertical distance, and coefficient of variation of vertical distance in response to different levels of trampling.[a]

Number of passes	Cryptogam cover (%)	Vertical distance (mm)	Coefficient of variation (%)
0	89 a	492 a	2.7 a
5	69 b	497 ab	1.9 b
15	45 c	505 bc	1.5 b
25	36 c	502 abc	1.4 b
50	9 d	511 c	1.4 b
250	0 d	511 c	1.4 b

[a] Any two values in the same column followed by the same letter are not significantly different (Duncan's multiple range test, $p = .05$).

Each lane was sampled along five transects oriented perpendicular to the lane and located 1 m apart. Each transect consisted of 10 measurement points 2 cm apart in the central part of the lane. At each point along the transect the vertical distance between a horizontal pipe, temporarily connecting the pipe at each end of the transect, and the ground surface was measured. Then the ground surface at that point was categorized as either bare soil or cryptogam.

These data provide three measures to evaluate disturbance. First, the vertical distances, a mean of 50 observations per lane, provide a measure of the degree to which crusts have been compressed by trampling. The variability of vertical distances across each transect provides an indication of surface roughness, which should decline with trampling. Roughness increases with crustal development and is important in reducing soil erosion. The measure used is the coefficient of variation of the vertical distances. Coefficients were calculated for each of the five transects across each lane and then averaged. The third measure is cryptogam cover, expressed as a percentage of the 50 ground surface observations for each lane. The significance of differences, between treatments and between years, was tested with analysis of variance and Duncan's multiple range test.

RESULTS

Cryptogamic crusts were immediately pulverized by trampling. Pedestals were flattened, and the black veneer of bacteria and cryptogams was obliterated. Changes in cryptogam cover, vertical distance, and the index of surface roughness were all statistically significant (Table 1). Differences between the effects of trampling with tennis shoes and boots were not significant, however.

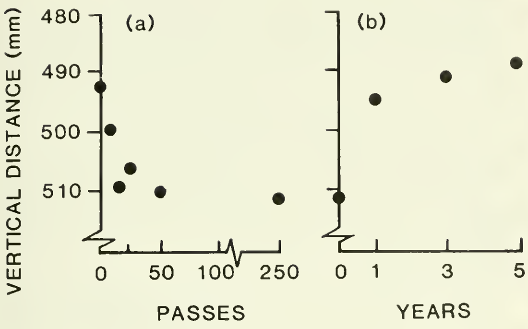

Fig. 2. Mean vertical distance from a horizontal transect to the ground surface (a) after different levels of trampling in lug-soled boots and (b) after one, three, and five years of recovery. Standards errors were all 2.2–2.8 mm.

TABLE 2. Cryptogam cover, vertical distance, and coefficient of variation of vertical distance 0, 1, 3, and 5 years following trampling.[a]

Years since trampling	Cryptogam cover (%)	Vertical distance (mm)	Coefficient of variation (%)
0	3 a	511 a	1.3 ab
1	20 b	499 b	1.0 a
3	71 c	491 c	1.9 b
5	85 d	490 c	1.9 b
Pre-trampling	89 d	492 c	2.7 c

[a] Any two values in the same column followed by the same letter are not significantly different (Duncan's multiple range test, $p = .05$).

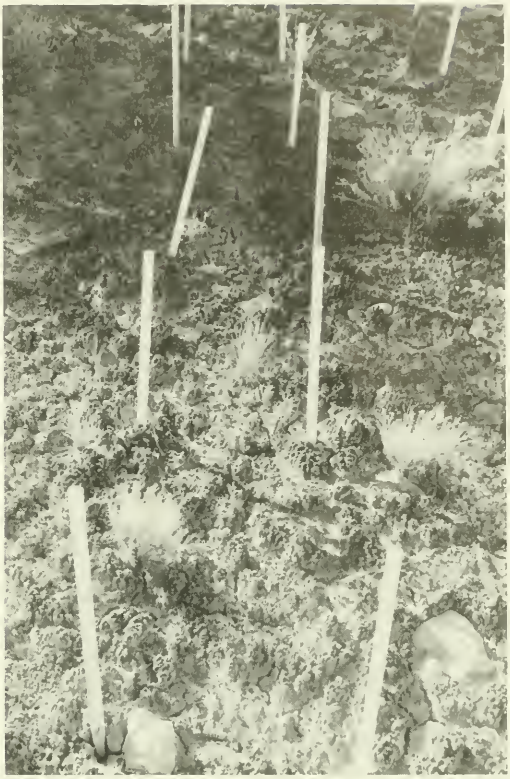

Fig. 3. The lane that received 250 passes in lug-soled boots after five years of recovery. View is from the end opposite that in Figure 1.

Cryptogam cover was reduced by 50% after 15 passes and was reduced to zero after 250 passes (Table 1). At this point the organisms were so widely dispersed that all visual evidence of their existence disappeared (Fig. 1). Destruction of pedestals also occurred rapidly (Fig. 2a). The vertical distance below the transect increased 13 mm following 15 passes. Additional trampling caused no significant further compression; the pedestals were already destroyed. Surface roughness, as measured by the mean coefficient of variation of the vertical distances, declined as the pedestals were pulverized (Table 1). All treatments were significantly different from the control, but not from each other. A blackened, irregular, aggregated soil surface was replaced after trampling by a flat surface of unconsolidated sands, which was much more vulnerable to erosion.

Substantial recovery occurred in the first year after trampling ceased. After one year of recovery, cryptogam cover had increased significantly (Table 2), and vertical distance had decreased significantly (Fig. 2b); however, surface roughness had not increased (Table 2). The unconsolidated sands left by trampling had reaggregated into a smooth, raised crust, but neither pedestals nor the blackened veneer of organisms had reformed. After three years of recovery, vertical distances were similar to pre-trampling levels. Cryptogam cover had increased dramatically, as had surface roughness, although both were still below pre-trampling values (Table 2). After five years of recovery, cryptogam cover had returned to pre-trampling levels. At this point all visual evidence of damage was gone (Fig. 3). Surface roughness values remained depressed (Table 2), however, suggesting that pedestals had not redeveloped fully.

The typical pattern of structural destruction and recovery is illustrated in Figure 4, which

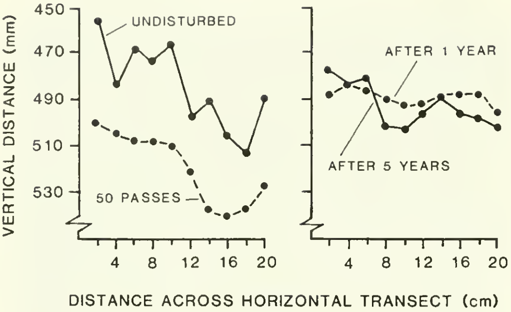

Fig. 4. Vertical distance from a horizontal transect to the ground surface (a) before trampling, (b) after 50 passes, (c) after one year of recovery, and (d) after five years of recovery. Data are for one of five transects across the lane trampled in tennis shoes.

shows the changes that occurred under one of the transects. Fifty passes with tennis shoes increased mean vertical distance and decreased variations between adjacent sample points. The redevelopment of a soil crust during the first year of recovery reduced vertical distance (i.e., the ground surface apparently rose), but surface irregularity remained low. After five years of recovery, the surface was more irregular than after trampling, but less irregular than before trampling.

DISCUSSION

These results illustrate the damage hikers can do to cryptogamic soil. The structure of these crusts was destroyed by only 15 passes, and cryptogam cover was negligible after only 50 passes. Compared with the response of vascular plants to similar levels of trampling disturbance, cryptogamic crusts are highly fragile but moderately resilient (Cole 1985, 1988). No other experimentally trampled vegetated surfaces have been denuded by such low levels of trampling.

Recovery was surprisingly rapid, however. This conclusion agrees with that of studies of recovery after grazing and fire (Johansen et al. 1984, Johansen and St. Clair 1986), which report more rapid and extensive recovery than anticipated. In this study recovery rates were probably increased by the close proximity of inoculum to the disturbed lanes and by the fact that disturbance occurred only once and was then removed. This study and previous ones rely primarily on visual criteria for evaluating recovery. The depressed surface roughness values five years after trampling suggest that complete recovery will take longer than five years. On disturbed sites at Canyonlands National Park such parameters as chlorophyll content, species diversity, and the thickness of the subsurface gelatinous sheaths that bind soil particles remain low even after crusts appear to have recovered (Belnap 1990).

The finding that the crustal surface rose during the first few years following the cessation of trampling is intriguing. The process by which pinnacled crusts develop is not well understood, but this result suggests that they may develop through accretion rather than erosion. If they were erosional features, the undisturbed strips should have remained conspicuously higher than the treatment lanes. This was not the case.

Given the fragility of these crusts, random trampling by backcountry recreationists is capable of seriously impacting large areas. Very low levels of ongoing use will maintain high levels of disturbance. This shows up most commonly as webs of trails that surround trail junctions, camping areas, and points of interest. In arid parks of the southwestern United States it is important to educate visitors about the nature, importance, and fragility of cryptogamic crusts. With this knowledge, visitors are more likely to voluntarily minimize trampling of crusts and support management actions taken to protect areas of crust. Most visitors neither recognize cryptogams as fragile vegetation nor realize their importance to site stability. It is also important to locate trails, camping areas, and other activity sites away from places with well-developed crust and, where this is not possible, to try to confine traffic to one well-developed route.

The one positive management implication of this research lies in the finding of relatively fast visual recovery. Where it is possible to eliminate trampling, crusts can quickly reestablish themselves. In this experiment trampling left an apparently sterile surface of sand that, in reality, was heavily inoculated with crustal organisms. Managers can speed recovery of disturbed areas by inoculating them (St. Clair et al. 1986). Moreover, even though complete recovery may take much more than five years, the rapid elimination of the visual evidence of damage is helpful. This makes it easier for managers to keep visitors off certain trails and campsites.

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EIMERIA SP. (APICOMPLEXA: EIMERIIDAE) FROM WYOMING GROUND SQUIRRELS (*SPERMOPHILUS ELEGANS*) AND WHITE-TAILED PRAIRIE DOGS (*CYNOMYS LEUCURUS*) IN WYOMING

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ABSTRACT.—Six species of the coccidian genus *Eimeria* (*E. larimerensis* [prevalence = 17%], *E. bilamellata* [12%], *E. beecheyi* [34%], *E. morainensis* [43%], *E. callospermophili* [21%], and *E. spermophili* [5%]) were recovered from Wyoming ground squirrels (*Spermophilus elegans elegans*) collected during 1983, 1984, 1985, and 1986. Infected ground squirrels were found to harbor from one to five species simultaneously. The 1007 hosts examined were collected from two different habitats: (1) a xeric desert shrub-steppe and (2) an irrigated alfalfa-brome field. All species of *Eimeria* occurred at each study site during all years, although the prevalence of each species varied between years. This is the first report of these congeries of species infecting this host. In a second study of sympatric populations of Wyoming ground squirrels and white-tailed prairie dogs (*Cynomys leucurus*), we found three species of *Eimeria* present in both host populations (*E. beecheyi* [white-tailed prairie dog prevalence = 83%, Wyoming ground squirrel = 52%], *E. morainensis* [22%, 52%], and *E. bilamellata* [17%, 10%]). This is the first report of these three species infecting white-tailed prairie dogs. *Eimeria larimerensis* was found in Wyoming ground squirrels but not in prairie dogs.

Levine and Ivens (1990) recently reported 17 species of *Eimeria* from ground squirrels of the genus *Spermophilus*. In most cases these species of *Eimeria* were described from small samples of hosts collected from restricted geographic locations, and only 1 or 2 species were recovered from the limited sample population of squirrels. They listed no species from the Wyoming ground squirrel, *Spermophilus elegans* Kennicott, 1863.

Additionally, Duszynski (1986) has reported that the host specificity of the coccidian genus *Eimeria* may be rather broad. For example, *Eimeria bilamellata* Henry, 1932 has been reported in nine species of ground squirrels (*Spermophilus* spp.) (Levine and Ivens 1990); and *E. larimerensis* Vetterling, 1964 has been found in five ground squirrel species, white-tailed prairie dogs (*Cynomys leucurus* Merriam, 1890) (Todd and Hammond 1968a), and black-tailed prairie dogs (*C. ludovicianus* Ord, 1815) (Vetterling 1964). Cross-transmission experiments with oocysts from prairie dogs inoculated into ground squirrels have been successful (Todd and Hammond 1968a, 1968b, Todd et al. 1968).

The purpose of this paper is to report the prevalence of six eimerian species in two populations of Wyoming ground squirrels occurring in two habitats and to report the eimerian parasites of sympatric populations of Wyoming ground squirrels and white-tailed prairie dogs.

METHODS

As part of an ongoing study on the life history of the Wyoming ground squirrel, 1007 individuals were examined for the presence of coccidian parasites of the genus *Eimeria* over a four-year period. These hosts were collected from two habitats: (1) xeric cold desert shrub-steppe, 14 km north of Baggs, Wyoming (107°45′W, 41°17′N) and (2) an irrigated alfalfa-brome field, 10 km south of Laramie, Wyoming (105°33′W, 41°12′N).

In late June and early July of 1983 and 1986 ground squirrels were snap-trapped in both study areas using three 40 × 50 trapping grids (0.6 ha) with traps set every 5 m (240 total traps). In 1984 and 1985 squirrels were randomly shot within the study sites throughout their summer active season (April–August). All squirrels were weighed, sexed, and necropsied. Fecal material was obtained during necropsy from the lower large intestine.

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The second study was initiated in conjunction with a white-tailed prairie dog study conducted by Menkens and Anderson (1989). The study area, located 11 km south of Laramie, Wyoming (105°40′W, 41°20′N), contained populations of both *C. leucurus* and *S. elegans* as well as a small population of 13-lined ground squirrels (*S. tridecemlineatus* Mitchill, 1821). A trapping grid of 11.3 ha containing 176 National live traps was established. Traps were baited with oats and opened before daylight each morning. After a four-hour trapping period the traps were closed for the remainder of the day. Trapped animals were weighed, sexed, and released; feces were collected from each trap following the animal's release. Trapping occurred over a five-day period, 3–7 July 1987.

All fecal samples collected in both studies were placed in 2% potassium dichromate solution at room temperature (25 C) for two to three weeks to allow oocyst sporulation for species identification. Sporulated oocysts were isolated by flotation in saturated sucrose flotation solution (specific gravity = 1.2) and identified at 100X objective with an Olympus (CH) compound microscope.

RESULTS

In the first study 613 ground squirrels were collected from the irrigated site and 394 from the xeric site. Six species of *Eimeria* were found infecting both populations. For the entire sample, 26% of the squirrels harbored one eimerian species, 26% had two species, 13% had three species, 2% had four, and only two animals were infected with five species simultaneously.

During the four-year sampling period, 168 of 1007 (17%) *S. elegans* examined were infected with *E. larimerensis*. Significantly more hosts were infected in the irrigated study site (23%) than in the xeric site (6%) (chi^2, $p \leq .01$) (Table 1).

Eimeria bilamellata was found infecting 11% of the squirrels examined. The prevalence of *E. bilamellata* varied among years and sites but there were never more than 21% of the hosts infected at any site during any year (Table 1). Overall, there was no significant difference in prevalence between the two sites over the four years (chi^2, $p \leq .10$).

Eimeria beecheyi Henry, 1932 was the second most prevalent species found during the study (34%), and for the four-year period the prevalence was higher in the alfalfa field (38% vs. 27%), but the difference was not significant (chi^2, $p \leq .10$) (Table 1).

Eimeria morainensis Torbett, Marquardt, and Carey, 1982 was the most prevalent species found during the study (43%). Significantly more hosts were infected with this species at the irrigated site (55% vs. 25%) during the four years (chi^2, $p \leq .01$) (Table 1).

Eimeria callospermophili Henry, 1932 was found infecting 21% of the squirrels examined. It was present in both populations, but no difference in prevalence was found between the two study sites over the four years (chi^2, $p \leq .10$) (Table 1).

Eimeria spermophili Hilton and Mahrt, 1971 was the least common species found during this study (5%). It occurred in only a few hosts from each study site, and no significant difference in prevalence occurred between the two sites (chi^2, $p \leq .10$) (Table 1).

In the second study a total of 69 *S. elegans*, 18 *C. leucurus*, and one *S. tridecemlineatus* were trapped over the five-day period. Of these, 47 *S. elegans* (68%) and 17 *C. leucurus* (94%) were positive for the presence of *Eimeria* oocysts. Thirty-six *S. elegans* (52%) and 15 *C. leucurus* (83%) were infected with *E. beecheyi*. Similarly, 36 *S. elegans* (52%) and 4 *C. leucurus* (22%) harbored *E. morainensis*. Three *C. leucurus* (17%) and 7 *S. elegans* (10%) were infected with *E. bilamellata*. *Eimeria larimerensis* infected 3 *S. elegans* (4%) and none of the 18 *C. leucurus*. Up to three eimerian species were found co-occurring in individual hosts.

DISCUSSION

Eimeria larimerensis was first described from *C. ludovicianus* from Larimer County, Colorado (Vetterling 1964). In 1968 this eimerian was reported by Todd and Hammond from an additional seven species of *Spermophilus*, including *S. armatus* Kennicott, 1863 from Utah and Montana; *S. variegatus* Erxleben, 1777 from Utah; *S. tridecemlineatus* from Wyoming; *S. lateralis* Say, 1823 from Utah; *S. beecheyi* Richardson, 1829 from California; *C. leucurus* Merriam, 1890 from Wyoming (Todd and Hammond 1968b); and

TABLE 1. Number and percentage of Wyoming ground squirrels (*Spermophilus elegans*) infected by *Eimeria* sp. by year. Samples ($N = 1007$) were taken from two habitats in Wyoming. Animals may be infected simultaneously by more than one species of *Eimeria*.

Species of *Eimeria*	1983				1984				1985			
	Mesic ($N = 314$)[a]		Xeric ($N = 212$)		Mesic ($N = 34$)		Xeric ($N = 72$)		Mesic ($N = 86$)		Xeric ($N = 74$)	
	No. of squirrels infected	%	No. of squirrels infected	%	No. of squirrels infected	%	No. of squirrels infected	%	No. of squirrels infected	%	No. of squirrels infected	%
larimerensis	53	17	12	6	10	29	8	11	8	9	4	5
bilamellata	35	11	7	3	2	6	8	11	17	20	1	1
beecheyi	45	14	26	12	7	21	22	31	37	43	45	61
morainensis	128	41	34	16	13	38	28	39	52	60	25	34
callospermophili	83	26	33	16	16	47	30	42	18	21	17	23
spermophili	19	6	4	2	6	18	2	3	2	2	8	10

Species of *Eimeria*	1986				Total			
	Mesic ($N = 179$)		Xeric ($N = 36$)		Mesic ($N = 613$)		Xeric ($N = 394$)	
	No. of squirrels infected	%	No. of squirrels infected	%	No. of squirrels infected	%	No. of squirrels infected	%
larimerensis	72	40	1	3	143	23	25[b]	6
bilamellata	37	21	1	3	91	15	26	7
beecheyi	143	80	13	36	232	38	106	27
morainensis	143	80	12	33	336	55	99[b]	25
callospermophili	16	9	0	0	133	22	80	20
spermophili	8	4	0	0	35	6	14	4

[a] Number of squirrels examined.
[b] Significant, $p < .01$.

S. spilosoma Bennett, 1833 from Colorado (Broda and Schmidt 1978). Experimentally, Todd and Hammond (1968b) inoculated what they called *S. richardsonii* Sabine, 1822 with *E. laramerensis*. Although all eight individuals developed "severe diarrhea" three to four days post-inoculation, no oocysts were recovered. *Spermophilus richardsonii* from Wyoming has since been elevated to specific status, *S. elegans*, by Zegers (1984).

Eimeria bilamellata was first described from *S. lateralis* in California (Henry 1932). It has been reported from *S. citellus* Linnaeus, 1766 in Hungary and Czechoslovakia (Pellerdy and Babos 1953), *S. franklinii* Sabine, 1822 from Iowa (Hall and Knipling 1935), *S. armatus* from Utah and Wyoming, *S. beecheyi* from California, and *S. variegatus* from Utah (Todd et al. 1968). Todd et al. (1968) were unable experimentally to infect *S. richardsonii* (syn. *S. elegans*) from Wyoming with sporulated oocysts from any of the above donor hosts.

Eimeria beecheyi was originally described from *S. beecheyi* collected in California Henry 1932). Since its first report, it has been found only in *S. relictus* in the USSR (Abenov and Svanbaev (1982).

Eimeria morainensis was first described by Torbett et al. (1982) from *S. lateralis* collected in northern Colorado. This is only the second report of the occurrence of *E. morainensis*.

Eimeria callospermophili was first described from *S. lateralis* in California (Henry 1932). More recently it has been reported from that same host in northern Colorado (Torbett et al. 1982). This species is widespread both in its host and geographical distribution, having been reported from *S. fulvus* Lichtenstein, 1823 and *S. maximus* Pallas, 1778 in the Soviet Union (Levine and Ivens, 1990), *S. spilosoma* from Mexico (Levine et al. 1957), *S. beldingi* Merriam, 1888 from California (Veluvolu and Levine 1984), *S. columbianus* Ord, 1815, *S. franklinii*, and *S. richardsonii* in Alberta, Canada (Hilton and Mahrt 1971). In addition, Todd and Hammond (1968a) found this species in six species of *Spermophilus* and *C. leucurus* (*S. armatus* from Utah and Montana, *S. richardsonii* from Montana and Wyoming [syn. *S. elegans*], *S. beecheyi* from California, *S. lateralis* and *S. variegatus* from Utah, and *S. tridecemlineatus* and *C. leucurus* from Wyoming).

Eimeria spermophili was first described by Hilton and Mahrt (1971) from *S. richardsonii* collected in Alberta, Canada. They also found this species in *S. franklinii* from the same area.

This is the first report of these six eimerian species infecting *S. elegans* and the first of *E. beecheyi*, *E. morainensis*, and *E. bilamellata* in *C. leucurus*.

In the first study, although the number of infected ground squirrels changed from year to year, the same species were present at both locations throughout the four-year period. The large sample collected from different habitats over a four-year period indicates that a single ground squirrel population can be infected with several species of *Eimeria*. With a few exceptions, the results of this study suggest that if intensive sampling were conducted with any of the other species of *Spermophilus*, more species of *Eimeria* would be found (Parker et al., in review).

Moreover, the known species of *Eimeria* may be considerably more widespread in their host distribution. As noted above, several reports of sharing of coccidian parasites between species within a genus and between different genera of sciurid hosts exist (Todd and Hammond 1968a, 1968b, Todd et al. 1968, Duszynski 1986). Veluvolu and Levine (1984) stated that an individual eimerian species may infect at least 11 host species. However, most previous coccidian surveys of host populations have reported a low species richness of the parasite community. Todd and Hammond (1968b) reported the presence of *E. larimerensis* in 5 species of *Spermophilus* and *C. leucurus*. They did not find this species in *S. elegans*, nor could they experimentally establish an infection in this species. This contrasts with the results of our first study in which we found 18% of the ground squirrels infected with this species. *Eimeria bilamellata* was also reported from a variety of ground squirrels by Todd et al. (1968), although they did not find this species in wild populations of *C. leucurus* or *S. richardsonii* (syn. *S. elegans*). These results also differ from ours in that we found 14% of 1007 *S. elegans* infected with this species. However, Shults (1986) could not experimentally establish infections in this host even after immunosuppression with corticosteroids for seven days prior to inoculation.

Eimeria morainensis and *E. beecheyi* are two of the most common protozoan parasites infecting *S. elegans*, but neither species has been previously reported from *C. leucurus*.

It is interesting to note that of the species of *Eimeria* originally described from *C. ludoviciani* by Vetterling (1964) (*E. ludoviciani*, *E. cynomysis*, *E. larimerensis*), and which have also been identified from *C. leucurus* in northwestern Wyoming (Seville and Williams, 1989), none were found in *C. leucurus* from our site.

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EMERGENCE, ATTACK DENSITIES, AND HOST RELATIONSHIPS FOR THE DOUGLAS-FIR BEETLE (*DENDROCTONUS PSEUDOTSUGAE* HOPKINS) IN NORTHERN COLORADO

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ABSTRACT.—Douglas-fir beetle–infested Douglas-fir trees were partially caged to determine the emergence period and beetle production. Beetles began emerging in April, but emergence peaked between 10 and 26 June. In 1987 and 1988 beetle emergence averaged 20 or more per sq. ft. of bark. Annual growth of the infested trees showed a decline prior to the beetle outbreak followed by an increase during the outbreak.

The Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, is usually an insignificant pest of Douglas-fir (*Pseudotsugae menziesii* [Mirb.] Franco) in the Front Range of Colorado. The beetle's life cycle generally lasts one year, although a partial second generation has been noted in other parts of its range. The beetle prefers windthrown trees but will infest standing trees during droughts or high population levels (Wood 1963). Standing trees also become more susceptible to infestation by the Douglas-fir beetle after severe defoliation by insects (Wright et al. 1984).

In 1972 western spruce budworm (*Choristoneura occidentalis* Freeman) populations began to increase in Roosevelt National Forest west of Fort Collins. Defoliation was noticeable, moderate, and limited to 3500 acres (1378 ha) in 1974 (Minnemeyer 1974), but by 1976, 54,000 acres (21,260 ha) were moderately to severely defoliated. Parts of Poudre Canyon, the location in this study, were severely defoliated (Cresap 1976). In 1977, the area of severe defoliation more than doubled on the forest (115,840 acres [45,606 ha]). Defoliation continually increased from 1977 until 1983, reaching a maximum of 469,000 acres (184,646 ha) (see Raimo 1983). Defoliation in Poudre Canyon, while noted as early as 1976, was confined to particular portions and was not extensive throughout until 1980 (see Linnane 1977, 1981). Thereafter, it was extensive and moderate to severe on most north-facing slopes until 1983–84.

Although the acreage of moderately to severely defoliated stands progressively increased from 1977 to 1983, egg mass densities peaked in 1980, four years prior to the maximum acreage defoliation, and had declined substantially by 1984 (see Raimo 1983, 1984). By 1985 population levels became endemic, with only light defoliation visible.

As the budworm outbreak subsided, Douglas-fir beetle populations began to increase. Scattered groups of faded trees were observed in the mid-1970s. Subsequently, beetle-killed Douglas-fir have increased both in numbers and in geographic extent (J. M. Schmid, personal observation). Numerous stands of Douglas-fir on north-facing slopes suffered significant tree mortality.

Because tree mortality became significant and our knowledge of the life history and habits of the Douglas-fir beetle in Colorado was deficient, the current infestations provided an opportunity to learn more about the beetle's life history and habits in Douglas-fir stands in Colorado and expanded our knowledge of the geographic variation in these aspects of the beetle's biology.

METHODS

To monitor beetle emergence, we attached 1 × 2-ft. (.3 × .6-m) wire screen emergence cages to infested trees in Poudre Canyon west of Fort Collins, Colorado, in late February 1987. Two cages were attached at breast height on each of five randomly selected

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1986-infested trees at each of three locations: the Narrows, Pingree Park road turnoff, and near BM 6998 (east of Indian Meadows). On April 3 another five trees near Crystal Lakes (northwest of Red Feather Lakes) were caged in the same manner.

To monitor emergence in 1988, we attached cages, as described above, to five 1987-infested trees on each of four sites: near Crystal Lakes (northwest of Red Feather Lakes) and in Poudre Canyon in late September 1987, and also near Camman Springs (south of Poudre Canyon) and near Black Mountain (north of Red Feather Lakes) in late October.

Cages were attached at breast height for practical purposes. Furniss (1962) recommended sampling for attack and brood densities at the midpoint on the bole because attack densities were twice as great there as at breast height, attack success was greatest in the midpoint zone, and live brood was greater. Furniss worked on standing trees that averaged 20 inches in diameter at breast height and ranged in height from 79 to 162 ft.; the sampling point on the average tree was thus 40 ft. or more aboveground. In contrast, our trees averaged 15 inches in diameter at breast height with trees only at the Pingree Park road site averaging 20 inches; tree height ranged from 34 to 88 ft. Although Furniss recommended sampling at or near the midpoint of the bole, it should be noted that he felled his trees for sampling and did not extract his samples from standing trees. In addition, the zone of optimum sampling is lower on smaller trees in the southern portion of the trees' range, i.e., southern Utah, than in Idaho, where Furniss did his study. Because our trees were smaller and were not to be felled, the terrain was difficult at some sites, and there was no evidence to suggest that the beetle's emergence pattern varied with height, we attached cages at breast height.

During 1987 and 1988, cages were checked at one- to two-week intervals from 1 April to 1 July. After 1 July, cages were checked at irregular intervals through September. During each check period, the number of emerging adults was recorded for each cage, and observations were made on the discoloration of foliage on the infested trees.

The density of emerging beetles per sq. ft. (.09 m^2) of bark surface was determined by dividing the total number of beetles emerging in each cage by the surface area covered by each cage (ca. 2 sq. ft. [.18 m^2]). Beetle numbers were subjected to one-way analysis of variance to determine if differences among locations were significant (alpha = .05). Beetle numbers at breast height were also tested against their respective tree diameters to determine if beetle production was related to tree diameter (DBH). For each year, tree diameters were grouped into three classes, and beetle numbers among diameter classes were tested for significant differences using analysis of variance (alpha = .05). For 1987 the diameter classes in inches (cm) were: 7.5–9.6 (19–24), 11.2–15.7 (31–61) and 16.2–24.3 (41–62). For 1988 diameter classes were: 9.3–12.5 (24–32), 12.6–13.3 (32–34), and 13.4–18.0 (34–46). Diameter classes differed between 1987 and 1988 because the diameters of the infested trees were different. A one-way ANOVA was used because all diameter classes were not equally present on all locations.

Population trend was evaluated by dividing the density of emerging beetles by twice the density of attacks (this assumes a pair of beetles creates each attack). When the ratio of emerging beetle density to attack density exceeds one, the beetle population is increasing. When the ratio is less than one, the population is decreasing.

The density of beetle attacks on standing trees was determined by removing 6 × 12-inch (15 × 30-cm) bark samples from or near breast height. Two samples were removed from each 1986-infested tree in late October 1987. Two samples from each 1987-infested tree were removed in late September 1987. The bark samples from 1987-infested trees were also used to determine brood density and stage of development.

To determine past growth rates of the 1986-infested trees, we extracted increment cores from the caged trees at breast height. Annual radial growth for each of the last 20 years was measured to .001 inch (.03 mm). Mean annual growth was determined for all trees from each of the four locations. Annual growth during the three preceding five-year periods (1972–76, 1977–81, 1982–86) was analyzed for significant differences in the periodic growth rate using one-way analysis of variance (alpha = .05). Separate one-way analysis of variance was used for each location because

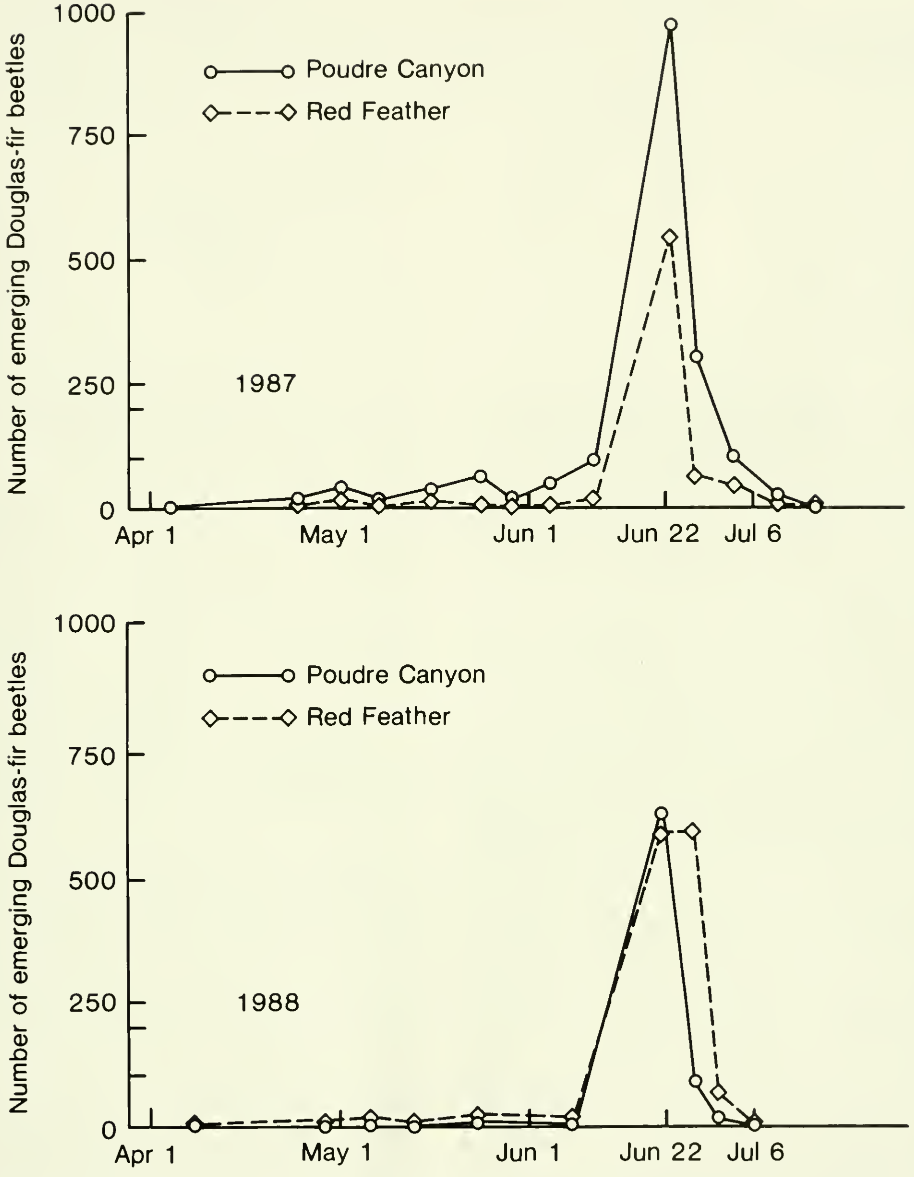

Fig. 1. Total number of Douglas-fir beetles emerging from five trees at four locations in the Arapaho-Roosevelt National Forest, Colorado, in 1987 and 1988.

the variability in site and stand conditions would not yield meaningful results in a more complex statistical design testing for differences among locations and their interactions. Periodic growth for the five-year periods was also used to compute Mahoney's PGR (Mahoney 1978), which is the ratio of the growth for one five-year period to the growth for the previous five years.

When analysis of variance indicated significant differences among the means, Tukey's test was used to determine which means were different (alpha = .05) (Steel and Torrie 1960).

RESULTS AND DISCUSSION

EMERGENCE.—Adults began emerging in mid-April of both years (Fig. 1), continuing to emerge at low rates until early June. Emergence peaked between 10 and 26 June in both

TABLE 1. Mean number of Douglas-fir beetles emerging per sq. ft. (.09 m^2) of bark for several locations in the Arapaho-Roosevelt National Forest. Within the same year, means followed by the same letter are not significantly different (alpha = .05).

Location	Number of trees 1987	Number of trees 1988	Cages per tree	Number of beetles ($\bar{x}$ ± S.D.) 1987	Number of beetles ($\bar{x}$ ± S.D.) 1988
Narrows	5	2	2	27 ± 14 a	
Pingree Park Road	5	2	2	40 ± 20 a	
BM 6998	5	5	2	21 ± 15 a	30 ± 28 ab
Crystal Lakes	5	5	2	39 ± 18 a	55 ± 33 a
Camman Spring		5	2		8 ± 10 b
Black Mountain		5	2		10 ± 11 b

years. Adults rarely emerged after 1 July. In terms of percentage of the emerging populations, 18% of the beetles had emerged by 10 June in 1987 and 4% in 1988; 77% and 92% emerged between 10 and 26 June in 1987 and 1988; 5% and 4% emerged after 26 June, respectively. After 1 July, 2% or less emerged in both years.

Wood (1963) noted two principal flight periods for the Douglas-fir beetle in California, Oregon, and Utah, depending on the overwintering life stage—one during May–June and another during July–August. In this study we found only one principal flight period. If a second flight period is occurring, we believe the beetles are reemerging adults, not new adults emerging later from the caged hosts.

DENSITY OF EMERGING ADULTS.—The number of adults emerging per sq. ft. (.09 m^2) of bark surface ranged from 6 to 82 in 1987 and 0 to 88 in 1988. Mean numbers per sq. ft. (.09 m^2) of bark showed significant variation among areas in 1987 and 1988, but Tukey's test did not reveal significant pairwise comparisons in 1987 (Table 1).

Although the number of emerging beetles did not significantly correlate with DBH, areas where mean tree diameter was 8.5 inches (22 cm) or less produced the lowest number of beetles. In addition, numbers were influenced by the density of attacks and tree diameter. The population trend ratio was generally >1 when attack densities were ≤12 per sq. ft. (.09 m^2) and tree diameter was >10 inches (25 cm) DBH. When tree diameter was <10 inches (25 cm), the trend ratio was <1. Similarly, when the density of attacks was >14 per sq. ft. (.09 m^2), the trend ratio was generally <1. Population trend thus appears to be influenced by competition (McMullen and Atkins 1961) and quantity of food (tree size, not number of trees) as hypothesized by Wright et al. (1984). Larger trees provide adequate food to produce an increasing population until the attack density exceeds 12 per sq. ft. (.09 m^2). At greater densities, competition causes beetle production to decrease. Smaller trees generally have production rates less than one, even when attack densities are 8–12 per sq. ft. (.09 m^2), because smaller trees do not provide sufficient phloem for developing larvae.

TABLE 2. Mean number of Douglas-fir beetles emerging per sq. ft. (.09 m^2) of bark by diameter class. Within the same year, means followed by the same letter are not significantly different (alpha = .05).

Diameter class (inches [cm])	Number of trees	Number of beetles ($\bar{x}$ ± S.D.)
	1987	
7.5 – 9.6 (19–24)	5	21 ± 15 a
11.2 – 15.7 (28–40)	7	36 ± 16 a
16.2 – 24.3 (41–62)	8	34 ± 21 a
	1988	
9.3 – 12.5 (24–32)	6	22 ± 25 a
12.6 – 13.3 (32–34)	7	20 ± 20 a
13.4 – 18.0 (34–46)	7	35 ± 38 a

Beetle densities in this study were about the same as or greater than those found by Fredericks and Jenkins (1988) in Logan Canyon, Utah. Beetle numbers of 21–22 per sq. ft. (.09 m^2) in our diameter classes of 7–13 inches (18–33 cm) were comparable to the beetle numbers at 22–24 per sq. ft. (.09 m^2) of Fredericks and Jenkins (1988). In trees of comparable diameters (i.e., 22 inches [56 cm]), beetle numbers of 34 per sq. ft. (.09 m^2) (Table 2) in this study were slightly greater than the 22–24 per sq. ft. (.09 m^2) of Fredericks and Jenkins (1988).

TABLE 3. Mean annual radial growth in .001 inch (.025 cm) for the periods 1972–76, 1977–81, and 1982–86 for the four 1987 locations. Within the same location, means followed by the same letter are not significantly different (alpha = .05).

	Mean annual growth (.001 inch) ($\bar{x}$ ± S.E.)		
Location	1972–76	1977–81	1982–86
Narrows	11 ± 1.0 a (28 ± 3)	12 ± 1.4 a (30 ± 4)	19 ± 1.3 b (48 ± 3)
Pingree Park Road	38 ± 2.3 a (97 ± 6)	30 ± 1.2 b (76 ± 3)	33 ± 1.2 ab (84 ± 3)
BM 6998	11 ± 0.9 a (28 ± 2)	7 ± 0.3 b (18 ± 1)	12 ± 1.8 a (30 ± 5)
Crystal Lakes	7 ± 0.6 ab (18 ± 2)	5 ± 0.3 b (13 ± 1)	8 ± 1.0 a (20 ± 3)

ATTACK DENSITIES.—The number of attacks per sq. ft. (.09 m^2) of bark surface ranged from 8 to 20 in 1986 and 6 to 14 in 1987. Within each location, attack densities were not significantly different between aspects. Mean densities ranged from 9 to 15 in 1986 and 8 to 10 in 1987, comparable to the fifth-year attack densities in Oregon of Wright et al. (1984). Because the Colorado outbreak appeared to be in its fifth year, the pattern of attack densities during the outbreak may be the same as in the Oregon outbreak. In contrast, attack densities from our Colorado locations were 62–80% lower than those of the Utah outbreak. In the recent outbreak in Utah, attack densities were high and essentially the same throughout the first three years (Fredericks and Jenkins 1988). Apparently, the Utah outbreak exhibited a pattern of attacks different from either the Oregon or Colorado outbreaks.

DISCOLORATION OF INFESTED TREES.—In February following the attack, foliage of most infested trees was predominantly green, only the lower two or three whorls of branches having discolored to red-brown. By late April most trees had discolored, the color ranging from yellow-green to reddish. By mid-May most trees were reddish. Trees with extensive woodpecker debarking and foliage discoloration in February turned reddish first, usually by late April. Those without these characteristics discolored later but had turned by May. Foliage usually discolored at different rates in different crown levels, the lower crown fading first. When it was yellow-green, the rest of the crown was green. When the upper crown yellowed, the lower crown was already reddish. From August through October, the best external clues for Douglas-fir beetle infestation were cinnamon-colored boring dust and/or clear pitch "streamers." During winter the most notable external characteristic was the debarked bole caused by woodpecker activity. These boles are lighter in color and can be discerned from more than 100 feet away. After October, but before the foliage turned red, woodpecker activity was the best characteristic for locating currently infested trees.

ANNUAL GROWTH.—Annual radial growth varied significantly among and within locations. Significant variation in growth among locations was expected because of differing site conditions, stand densities, and tree ages. In three of four locations, mean annual growth declined significantly in the 1977–81 period, presumably a result of the budworm outbreak (Table 3). Mean annual radial growth in each location increased during 1982–86. Thus, the increase in Douglas-fir beetle populations coincided with increasing growth of the host.

Mean annual growth for the 1977–81 period ranged from .005 inch to .03 inch (.013 to .08 cm) and for 1982–86 from .008 to .033 inch (.02 to .08 cm) (Table 3). The growth rate was greatest on large trees situated in a ravine, a more favorable site.

The periodic growth ratio (PGR) exhibited changes similar to the changes in mean annual radial growth. In three of four locations, PGR became <1 when 1977–81 was compared against 1972–76. PGR then became >1 when 1982–86 was compared with 1977–81. Growth rates declined for 1977–81 because of the budworm defoliation; thus, the change in PGR for 1977–81 vs. 1972–76 was expected. However, the increase in Douglas-fir beetle populations with >1 PGR for the 1982–86 period was unexpected. Most stands susceptible to the mountain pine beetle (*D. ponderosae* Hopkins) exhibit PGRs <1, and so a beetle outbreak coinciding with a period of increasing growth is unusual.

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ECOLOGICAL REVIEW OF BLACK-TAILED PRAIRIE DOGS AND ASSOCIATED SPECIES IN WESTERN SOUTH DAKOTA

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ABSTRACT.—Black-tailed prairie dogs (*Cynomys ludovicianus*) once occupied extensive areas throughout the Great Plains. In recent years massive control programs have been initiated to reduce prairie dog populations, primarily to benefit the livestock grazing industry. Currently in western South Dakota most prairie dogs are found on public lands. Control programs using toxicants for prairie dogs have been found to be economically unfeasible when not combined with reductions in livestock grazing. Control programs also have negatively impacted some nontarget species of birds and small mammals. Livestock grazing is directly related to prairie dog densities. Prairie dog and livestock grazing activities are responsible for keeping plant phenological development in a suppressed vegetative stage with higher nutritional qualities that attract greater herbivore use. Prairie dog colonies create and enhance habitat for many wildlife species; in western South Dakota 134 vertebrate wildlife species have been documented on prairie dog towns. Scientific evidence strongly suggests that prairie dogs are valuable components of the prairie ecosystem. They are responsible for maintaining, creating, and regulating habitat biodiversity through soil and vegetative manipulation for a host of vertebrate and invertebrate species dependent upon prairie dog activity for their survival.

Quantified information regarding vertebrate wildlife species living on or closely associated with black-tailed prairie dog (*Cynomys ludovicianus*) colonies is lacking or is only alluded to in scientific literature. To promote a better understanding of the complexity of prairie dogs and their habitat requirements and their importance to vertebrate species of wildlife, we conducted a review of scientific literature regarding prairie dog biology, ecology, and associated biopolitics pertaining to land management practices. Most of the studies and observations reported in this paper were conducted in western South Dakota. Where possible, corroborating studies and literature from other areas are presented and their importance discussed.

HISTORICAL BACKGROUND

Historically, prairie dogs occupied extensive areas on the Great Plains, ranging from Texas to Saskatchewan (Hall 1981) (Fig. 1). Merriam (1902) noted that prairie dogs compete with livestock for forage and are systematically targeted for elimination by livestock producers. The largest areas of land in the United States currently occupied by prairie dogs are federally managed lands (Schenbeck 1982). In South Dakota most black-tailed prairie dogs are found on lands administered by USDA Forest Service, primarily the Buffalo Gap National Grasslands and Fort Pierre National Grasslands (Schenbeck 1982). Storch (1989) estimated that prairie dogs inhabited 3,000 acres on the South Dakota portion of the Nebraska National Forest in the 1960s. In the mid-1970s prairie dogs inhabited approximately 20,000 acres on the Conata Basin portion of the grasslands (Schenbeck 1982); Schenbeck's estimate represents an 87% increase over an eight-year period. The livestock grazing industry claimed estimated losses of up to \$10.29 per acre on pasture and rangeland and \$30.00 per acre for hayland on a statewide basis (Dobbs 1984) and objected to the increase in prairie dogs.

ECONOMICS OF CONTROL AND LIVESTOCK GRAZING

The South Dakota livestock industry has recommended and instigated widespread wholesale reductions in prairie dog densities on public land, and in 1983 the state legislature listed the prairie dog as a pest and predator (Clarke 1988). Of the 707,000 acres in the Ft. Pierre and Buffalo Gap National Grasslands,

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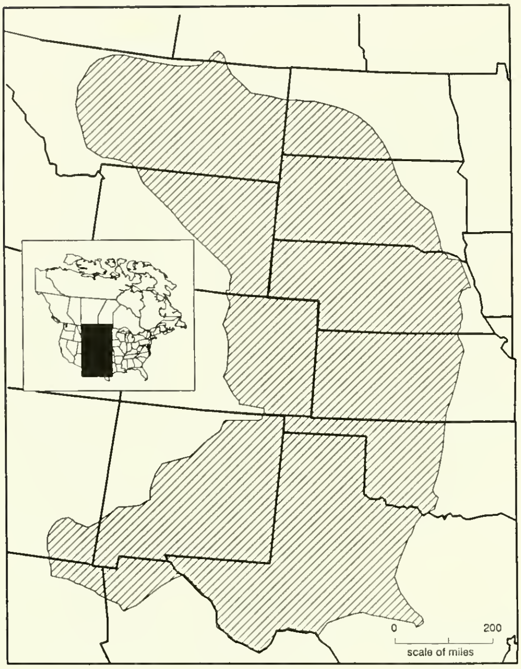

Fig. 1. Distribution of black-tailed prairie dog (*Cynomys ludovicianus*) on the Great Plains (adapted from Hall 1981).

approximately 10,000 acres are currently occupied by prairie dogs (Storch 1989). Control of prairie dogs has usually been initiated without consideration of the value of forage gained (Collins et al. 1984) or the effect on wildlife species associated with prairie dogs and their habitat (Sharps 1988).

An economic analysis of prairie dog control by Collins et al. (1984) found it was not economically feasible to poison prairie dogs in the Conata Basin using zinc phosphide because the annual control costs exceeded the value of forage gained. Also, based on burrow counts, prairie dog densities were significantly less on areas excluded to cattle than on areas grazed by cattle (Uresk et al. 1982). Herbicide applications to reduce forb production and thus reduce prairie dog densities were also found to be an inefficient control method because prairie dogs changed their diets from forbs to grasses (Fagerstone et al. 1977). It has long been known and extensively reported that cattle grazing will influence and is directly proportional to prairie dog densities (Koford 1958, Knowles 1982, Uresk et al. 1982, Cincotta 1985, Snell 1985). Schenbeck (1986) reported that habitat suitability for prairie dogs can be reduced by combining rodenticide use with changes in livestock grazing practices.

The poison bait effects of zinc phosphide- and strychnine-treated oats on nontarget birds, small mammals, and other nontarget species were evaluated by Uresk et al. (1988). The effects on nontarget bird species showed varied losses to Horned Larks, depending upon the density of strychnine-treated oats used, with no losses to other avian seedeaters. No measurable reductions in Horned Larks were found using zinc phosphide-treated oats, although there were indirect impacts on Horned Larks resulting from habitat changes. Prairie dog towns provide habitat for many seed-eating and insectivorous birds. Significantly, Apa (1985) reported that 50 species of birds were observed using prairie dog towns during the course of his study.

While zinc phosphide may not be detrimental to Horned Larks and the smaller seed-eating birds, it has been reported to be relatively toxic to gallinaceous birds (Record and Swick 1983).

Studies by Koford (1958), Smith (1958), Snell and Hlavacheck (1980), and Uresk et al. (1982) indicated that excluding or decreasing cattle grazing increases cool-season grass density (wheatgrass and needlegrass) and reduces prairie dog colony size on mid- and short-grass rangeland. This method of prairie dog control has historically been opposed or rejected by the livestock grazing community. Although heavily grazed rangelands give rise to very slow forage improvement, prairie dogs alone are generally not responsible for range deterioration (Uresk 1987). Prairie dog expansion is related to livestock grazing (Uresk et al. 1982, Uresk and Bjugstad 1983). Black-tailed prairie dogs usually disperse during May and June and have been reported to move and become established an average of three miles from their original towns (Garrett and Franklin 1981, Cincotta et al. 1987). They will repopulate their towns to initial population numbers in three years (Schenbeck 1982, Cincotta et al. 1987). Economically, control of prairie dogs is not feasible except at very low maintenance levels—below 5%—based on an increase of forage for livestock of only 50 pounds per acre, a 4.4% increase (Uresk et al. 1982, Collins et al. 1984, Uresk 1985, 1986).

ASSOCIATED VERTEBRATE SPECIES

Prairie dogs create a biological niche or habitat for many species of wildlife (King 1955, Reading et al. 1989). Agnew et al. (1986) found that bird species diversity and rodent abundance were higher on prairie dog towns than on mixed-grass prairie sites. The high diversity of bird species was attributed to heterogeneous plant cover and species composition (Agnew et al. 1986, Cincotta et al. 1987). In a survey of prairie dog towns extending through portions of Utah, Colorado, and New Mexico, Clark et al. (1982) recorded 107 vertebrate species and subspecies of wildlife; more species were associated with larger prairie dog towns than with smaller towns. Sixty-four vertebrate wildlife species were recorded by Campbell and Clark (1981) on 25 white-tailed and 21 black-tailed prairie dog colonies in Wyoming. Reading et al. (1989) listed 163 vertebrate species sighted on black-tailed prairie dog colonies. They suggest that "richness of associated vertebrate species on black-tailed prairie dog colonies increases with colony size and regional colony density."

Data pertaining to vertebrate wildlife species associated with black-tailed prairie dog colonies were obtained from an extensive literature review, personal field notes (J. C. Sharps, unpublished), observations while conducting endangered species surveys, or observations incidental to other research on prairie dog colonies. In South Dakota, 600 vertebrate wildlife taxa were found statewide. There are 332 species located west of the Missouri River (excluding fish) (Sharps and Benzon 1984). Of western wildlife species, 40% were found to be associated with prairie dog colonies. This 40% represents 134 vertebrate wildlife species (Table 1) associated with prairie dog colonies in western South Dakota: 88 birds, 36 mammals, 6 reptiles, and 4 amphibians (Agnew 1983, Apa 1985, MacCracken et al. 1985, Agnew et al. 1986, Uresk et al. 1986, Deisch et al. 1989). Whitney et al. (1978) reported that approximately 33 bird species, or 39% of the birds found in South Dakota, are conspicuous on the grasslands. Of those 33 species only 5, or approximately 15%, were not observed or reported on prairie dog colonies.

PLANT-SOIL-ANIMAL INTERACTIONS

Agnew et al. (1986) and Deisch et al. (1989) found five classes of invertebrates on prairie dog colonies located on the Badlands National Park and Buffalo Gap National Grasslands, respectively. The five classes consisted of Insecta (6 orders, 26 families), Arachnida (4 orders, 10 families), Chilopoda, Diplopoda, and Crustacea. Agnew et al. (1988) found that insectivorous rodent species favor prairie dog colonies; these mammals, by consuming arthropods, may reduce localized arthropod outbreaks.

Prairie dog colonies provide habitat diversity in the prairie ecosystem by mixing soils and regulating vegetative species diversity (Koford 1958, Bonham and Lerwick 1976, Agnew et al. 1986, Detling and Whicker 1988, Sieg 1988). This in turn creates interactions and numerous niches, thereby contributing to the food chain for a host of invertebrate and vertebrate wildlife species. Prairie dogs alter soil structure and chemical composition by their burrowing activities, excrement, and addition of plant material, which contribute to vegetation diversity (Gold 1976, Hansen and Gold 1977, O'Meilia et al. 1982, Cincotta 1985, Agnew et al. 1986). Prairie dog activity results in the aeration, pulverization, granulation, and transfer of considerable quantities of soil (Buckman and Brady 1971, Sieg 1988). Soils in prairie dog colonies are richer in nitrogen, phosphorus, and organic matter than soils in adjacent grasslands. Sheets et al. (1971) found prairie dog and cattle feces, grass seeds, stolons, roots, and remains of prairie dogs and mice while excavating 18 prairie dog burrows to retrieve black-footed ferret scats in south central South Dakota. Soil-enrichment activity of the prairie dog is beneficial to the macroarthropods living in the soil. Forbs and grasses in prairie dog colonies are constantly clipped by prairie dogs and remain in a state of regrowth (O'Meilia et al. 1982, Cincotta 1985). Ingham and Detling (1984) reported that prairie dog colonies support higher populations of nematodes than adjacent areas away from the colonies. They also stated that prairie dog activities suppress plant phenological development, thus maintaining the plants in a vegetative state. Young vegetation, which is higher in nutritional qualities than mature plants, attracts cattle, bison, and pronghorn to prairie dog colonies (Uresk and Bjugstad 1983, Coppock et al. 1983, Knowles 1986, Krueger 1986, Detling and Whicker 1988).

TABLE 1. Vertebrate wildlife species associated with black-tailed prairie dog colonies in western South Dakota.

Eastern tiger salamander	*Ambystoma tigrinum tigrinum*
Great plains toad	*Bufo cognatus*
Western chorus frog	*Pseudacris triserata*
Bullfrog	*Rana catesbeiana*
Turtles	Emydidae ukn spp.
Lizards	Iguanidae ukn spp.
Plains garter snake	*Thamnophis radix*
Smooth green snake	*Opheodrys vernalis*
Bullsnake	*Pituophis melanoleucus sayi*
Prairie rattlesnake	*Crotalus viridis viridis*
Great Blue Heron[a]	*Ardea herodias*
Trumpeter Swan[a]	*Cygnus buccinator*
Canada Goose[a]	*Branta canadensis*
Mallard[a]	*Anas platyrhynchos*
Gadwall[a]	*A. strepera*
Northern Pintail[a]	*A. acuta*
Blue-winged Teal[a]	*A. discors*
Northern Shoveler[a]	*A. clypeata*
Canvasback[a]	*Aythya valisineria*
Turkey Vulture[b]	*Cathartes aura*
Red-tailed Hawk[b]	*Buteo jamaicensis*
Swainson's Hawk[b]	*B. swainsoni*
Rough-legged Hawk[c]	*B. lagopus*
Ferruginous Hawk[b]	*B. regalis*
Golden Eagle[b]	*Aquila chrysaetos*
Bald Eagle[d]	*Haliaeetus leucocephalus*
Northern Harrier[b]	*Circus cyaneus*
Prairie Falcon[b]	*Falco mexicanus*
Merlin[c]	*F. columbarius*
American Kestrel[b]	*F. sparverius*
Sharp-tailed Grouse[b]	*Tympanuchus phasianellus*
Ring-necked Pheasant[c]	*Phasianus colchicus*
Sora[a]	*Porzana carolina*
Killdeer[b]	*Charadrius vociferus*
Long-billed Curlew[b]	*Numenius americanus*
Upland Sandpiper[b]	*Bartramina longicauda*
Long-billed Dowitcher[a]	*Limnodromus scolopaceus*
Wilson's Phalarope[a]	*Phalaropus tricolor*
Ring-billed Gull[c]	*Larus delawarensis*
Rock Dove[b]	*Columba livia*
Mourning Dove[b]	*Zenaida macroura*
Great-horned Owl[b]	*Bubo virginianus*
Snowy Owl[d]	*Nyctea scandiaca*
Burrowing Owl[b]	*Athene cunicularia*
Short-eared Owl[b]	*Asio flammeus*
Common Nighthawk[b]	*Chordeiles minor*
Belted Kingfisher[e]	*Ceryle alcyon*
Northern Flicker[b]	*Colaptes auratus*
Red-headed Woodpecker[b,e]	*Melanerpes erythrocephalus*
Downy Woodpecker[e]	*Picoides pubescens*
Eastern Kingbird[b]	*Tyrannus tyrannus*
Western Kingbird[b]	*T. verticalis*
Say's Phoebe[b]	*Sayornis saya*
Horned Lark[b,d]	*Eremophila alpestris*
Violet-green Swallow[b]	*Tachycineta thalassina*
Northern rough-winged Swallow[b]	*Stelgidopteryx serripennis*
Barn Swallow[b]	*Hirundo rustica*
Cliff Swallow[b]	*H. pyrrhonota*
Blue Jay[c]	*Cyanocitta cristata*
Black-billed Magpie[b]	*Pica pica*
Common Raven[b]	*Corvus corax*
American Crow[b]	*C. brachyrhuchos*
Northern Mockingbird[c]	*Mimus polyglottos*
Gray Catbird[b]	*Dumetella carolinensis*
American Robin[b]	*Turdus migratorius*
Eastern Bluebird[c]	*Sialia sialis*
Mountain Bluebird[b]	*S. currucoides*
Water Pipit[c]	*Anthus spinoletta*
Northern Shrike[d]	*Lanius excubitor*
Loggerhead Shrike[b]	*L. ludovicianus*
European Starling[b]	*Sturnus vulgaris*
Yellow Warbler[b]	*Dendroica petechia*
Common Yellowthroat[b]	*Geothlypis trichas*
Yellow-breasted Chat[b]	*Icteria virens*
House Sparrow[b]	*Passer domesticus*
Bobolink[b]	*Dolichonyx oryzivorus*
Western Meadowlark[b]	*Sturnella neglecta*
Yellow-headed Blackbird[c]	*Xanthocephalus xanthocephalus*
Red-winged Blackbird[b]	*Agelaius phoeniceus*
Brewer's Blackbird[b]	*Euphagus cyanocephalus*
Common Grackle[b]	*Quiscalus quiscula*
Brown-headed Cowbird[b]	*Molothrus ater*
Western Tanager[b]	*Piranga ludoviciana*
Dickcissel[b]	*Spiza americana*
Common Redpoll[d]	*Carduelis flammea*
Pine Siskin[b]	*C. pinus*
American Goldfinch[b]	*C. tristis*
Rufous-sided Towhee[b]	*Pipilo erythrophthalmus*
Lark Bunting[b]	*Calamospiza melanocorys*
Grasshopper Sparrow[b]	*Ammodramus savannarum*
Vesper Sparrow[b]	*Pooecetes gramineus*
Lark Sparrow[b]	*Chondestes grammacus*
Slate-colored Junco[d]	*Junco hyemalis*
Oregon Junco[c]	*J. oreganus*
Chipping Sparrow[b]	*Spizella passerina*
White-crowned Sparrow[c]	*Zonotrichia leucophrys*
McCown's Longspur[c]	*Calcarius mccownii*
Chestnut-collared Longspur[b]	*C. ornatus*
Shrews	Soricidae ukn. spp.
Bats	Vespertilionidae ukn. spp.
Eastern cottontail	*Sylvilagus floridanus*
Desert cottontail	*S. auduboni*
White-tailed jackrabbit	*Lepus townsendii*
Black-tailed jackrabbit	*L. californicus*
Thirteen-lined ground squirrel	*Spermophilus tridecemlineatus*
Black-tailed prairie dog	*Cynomys ludovicianus*
Northern pocket gopher	*Thomomys talpoides*
Plains pocket gopher	*Geomys bursarius*
Olive-backed pocket mouse	*Perognathus fasciatus*
Hispid pocket mouse	*P. hispidus*
Ord's kangaroo rat	*Dipodomys ordii*
Plains harvest mouse	*Reithrodontomys montanus*
Western harvest mouse	*R. megalotis*
Deer mouse	*Peromyscus maniculatus*
Northern grasshopper mouse	*Onychomys leucogaster*

TABLE 1 continued.

Prairie vole	*Microtus ochrogaster*
Norway rat	*Rattus norvegicus*
House mouse	*Mus musculus*
Porcupine	*Erethizon dorsatum*
Raccoon	*Procyon lotor*
Long-tailed weasel	*Mustela frenata*
Black-footed ferret	*M. nigripes*
Mink	*M. vison*
Badger	*Taxidea taxus*
Spotted skunk	*Spilogale Putorius*
Striped skunk	*Mephitis mephitis*
Coyote	*Canis latrans*
Red fox	*Vulpes vulpes*
Northern swift fox	*Vulpes velox hebes*
Bobcat	*Lynx rufus*
Mule deer	*Odocoileus hemionus*
White-tailed deer	*O. virginianus*
Pronghorn	*Antilocapra americana*
Bison	*Bison bison*

[a] Birds associated with wet years.
[b] Breeding birds.
[c] Transient birds.
[d] Wintering birds.
[e] Birds in riparian habitat adjacent to prairie dog colonies.

IMPORTANCE OF PRAIRIE DOG COLONIES TO ASSOCIATED WILDLIFE

Prairie dog colonies attract many insectivorous and carnivorous birds and mammals because of the concentration of numerous prey species (Clark et al. 1982, Agnew et al. 1986, Agnew et al. 1988). Hillman (1968) reported that prairie dogs are the principal food source of black-footed ferrets. Ferret decline has been attributed to prairie dog control practices and agricultural land use changes (Hillman and Clark 1980). Swift fox were found to have their dens on or within 0.8 km of prairie dog colonies (Hillman and Sharps 1978). The major portion of the swift fox diet is prairie dogs, 49%, and insects, 27% (Uresk and Sharps 1986). Raptors are particularly attracted to South Dakota prairie dog colonies. Juvenile Snowy Owls and Bald Eagles have been observed utilizing prairie dog colonies during the winter months; Golden Eagles can be found near prairie dog colonies all year; Ferruginous Hawks, Red-tailed Hawks, Kestrels, Prairie Falcons, Harriers, Rough-legged Hawks, Short-eared Owls, and Burrowing Owls use prairie dog colonies in the spring, summer, and fall months. Great-horned Owls have been observed hunting for cottontails and jackrabbits on prairie dog colonies at night. The principal mammalian predator species observed on prairie dog colonies are coyote, badger, and bobcat (Hillman and Sharps 1978).

Scientific evidence strongly suggests that prairie dogs are valuable components of the prairie ecosystem. Their burrowing activities and feeding habits are directly responsible for creating habitat diversity and thus providing a niche for 134 vertebrate wildlife species and over 36 families of invertebrate fauna (Agnew 1983, Deisch et al. 1989). Clark (1968) stated:

> prairie dogs have been in the grassland community for at least 1,000,000 years, probably occurring in great numbers; it would seem that if prairie dogs were detrimental they would have long ago destroyed the community of which they are a part.

SUMMARY

Prairie dogs were once significantly more numerous on public lands in South Dakota than they are today. Massive control programs have been initiated with little or no thought to the biological importance and ecological role of the prairie dog in the prairie ecosystem. Studies of prairie dog biology and ecology have shown that prairie dogs are not as detrimental as once believed to the livestock grazing industry. Studies have also shown that prairie dogs are extremely important to the ecosystem because they provide habitat and vegetation diversity in the prairie biome. Field observations and studies found 134 species and subspecies of vertebrate wildlife associated with prairie dog colonies in western South Dakota.

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EFFECTS OF PRAIRIE DOG RODENTICIDES ON DEER MICE IN WESTERN SOUTH DAKOTA

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ABSTRACT.—Mortality of nontarget small mammals was determined after application of three black-tailed prairie dog (*Cynomys ludovicianus*) rodenticide treatments (prebaited zinc phosphide, prebaited strychnine, and strychnine alone) in western South Dakota. Immediate (September 1983) and long-term (September 1983 through August 1984) impacts on deer mouse (*Peromyscus maniculatus*) relative densities were evaluated, and the three rodenticide treatments were compared for efficacy. The three treatments had no significant ($\alpha < .10$) immediate impacts on deer mouse relative densities, although zinc phosphide did lower them; that impact was not, however, long term. Long-term impacts of the two strychnine treatments were variable, with an increase in deer mouse densities with the strychnine only treatment. Overall, comparisons among the three treatments indicated that zinc phosphide was more effective than either strychnine treatment in reducing deer mouse densities.

Considerable time and money have been spent on control of prairie dogs to reduce the agricultural damage they cause (Collins et al. 1984). However, efforts to evaluate the impact of prairie dog control methods on the total biotic communities of prairie dog towns have been limited. For example, immediate and long-term rodenticidal effects on nontarget wildlife such as deer mice (*Peromyscus maniculatus*) have not been fully evaluated. Appliers, when selecting toxic baits, often overlook information on the margin of safety to nontarget wildlife.

Small mammals are important components of prairie dog towns. Their fossorial activities mix and enrich soils; their food habits may affect vegetation, seed, and invertebrate distribution and abundance; and they provide a food base for predators. When small mammals ingest rodenticides used to control prairie dogs, incidental loss may change the ecological balance on prairie dog towns.

Rodenticides, in addition to causing direct mortality to nontarget wildlife, may impact them indirectly by removing or reducing prairie dog populations. Prairie dogs create niches for small mammals in rangeland ecosystems (Koford 1958, Allen 1967, O'Meilie et al. 1982, MacCracken et al. 1985, Agnew et al. 1986). For example, prairie dogs act as ecosystem regulators by maintaining habitat suitable for some small mammals, such as deer mice, that are associated with sparse, heterogeneous vegetative cover. Prairie dog burrows provide security cover and nesting habitat for small mammals. When prairie dog activity ceases, burrows are no longer maintained, soil erodes into the holes, and vegetation recaptures the mounds (Klatt 1971, Potter 1980).

Rodenticides used for prairie dog control include zinc phosphide and strychnine. Zinc phosphide is an acute rodenticide that appears to have limited environmental impact (Hilton et al. 1972). Its increased use in recent years (Schenbeck 1982) has resulted in improved formulations and application rates (Tietjen 1976). Secondary poisoning from zinc phosphide poses minimal threat to predators and scavengers that feed on poisoned rodent carcasses (Bell and Dimmick 1975, Schitoskey 1975, Hegdal et al. 1981).

Nontarget wildlife that consume strychnine bait or strychnine-poisoned carcasses are at risk (Rudd and Genelly 1956, Schitoskey 1975, Hegdal and Gatz 1977, Deisch et al. 1989). Apa (1985), in a companion study, found that strychnine used for prairie dog control reduced Horned Lark (*Eromophila alpestrus*) densities.

Little information is available on repopulation of small mammals following rodenticide treatment (Wood 1965). Such information is needed to formulate guidelines for federal, state, and private landowners for minimizing nontarget wildlife losses caused by prairie dog rodenticides. A program to control black-tailed prairie dogs (*Cynomys ludovicianus*) in western South Dakota provided us the opportunity to assess and compare immediate (direct) and long-term (indirect) impacts on deer mouse densities of three prairie dog control treatments: prebaited zinc phosphide, prebaited strychnine, and strychnine alone.

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STUDY AREA

This study was conducted on the Buffalo Gap National Grasslands and in the Badlands National Park of western South Dakota at elevations of 820–900 m. Geological formations consisted of sharp pinnacles, towers, steep gorges, and faults. Vegetated tabletop buttes and gently rolling mixed grasslands scattered throughout the area supported prairie dog towns.

The National Grasslands, located in Conata Basin, is grazed by cattle from mid-May to late October each year. Native herbivores include black-tailed (*Lepus californicus*) and white-tailed jackrabbit (*L. townsendii*), eastern cottontail (*Sylvilagus floridanus*), pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), and various small mammals. The Badlands National Park excludes cattle, but American bison (*Bison bison*) are present.

Dominant grasses are western wheatgrass (*Agropyron smithii*), blue grama (*Bouteloua gracilis*), buffalograss (*Buchloe dactyloides*), and needleleaf sedge (*Carex eleocharis*). Prairie dogweed (*Dysodia papposa*), Patagonia Indianwheat (*Plantago patagonica*), buckhorn (*Plantago spinulosa*), scarlet globemallow (*Sphaeralcea coccinea*), and prostrate bigbract verbena (*Verbena bracteata*) are dominant forbs.

Climate is semiarid-continental with extremely cold winters and hot, fluctuating summer temperatures. Average annual precipitation is 39.7 cm, most of which falls as high-intensity thundershowers from April through September.

METHODS AND MATERIALS

Small mammals were sampled from May through October 1983 (pretreatment) and May through August 1984 (posttreatment). Eighteen permanent 100 × 100-m (1.0-ha) sampling sites were established on 15 prairie dog towns. Rodenticide treatments were clustered into three separate groups to prevent cross-contamination with respect to wide-ranging nontarget species (6 sites per rodenticide treatment) 13 and 16 km apart. Each rodenticide treatment had 3 control and 3 treated sites. Only zinc phosphide treatments were applied to the park sites because strychnine use is forbidden. Prebaited strychnine and strychnine alone were applied to the grasslands sites.

Relative densities of small mammals (unique mammals/trap session) were determined for each of the 18 sites. A trapping grid included 64 Sherman live traps 10 m apart and a 10-m buffer border. Trapping began in May of each year and continued at four-week intervals. Each trap session consisted of one night of prebaiting followed by four consecutive nights of trapping (256 trap nights/session). Traps were baited with a peanut butter–rolled oats mixture. Captured rodents were identified to species, assigned a unique number by toe amputation (Taber and Cowan 1969), then released. Density was measured as the number of unique captures.

Rodenticides and Bait Application

Steam-rolled oats used for prebait and poisoned baits were formulated at the U.S. Fish and Wildlife Service Pocatello Supply Depot. Zinc phosphide was applied to steam-rolled oats at a concentration of 2.0% by weight active ingredients. (Alcolec S, used as an adhesive, was made by American Lecithin Co., Inc.) Strychnine alkaloid was applied to oats at 0.5% by weight. Nontreated steam-rolled oats (4 g) were applied as prebait for zinc phosphide and for one strychnine treatment during 20–21 September 1983. Prebaited areas were visited prior to baiting to assure that most of the prebait had been consumed. Active rodenticides on oats (4 g) were applied three days after prebaiting (22–24 September 1983) in accordance with federal instructions. Both prebait and rodenticides were applied from bait dispensers affixed to Honda 3-wheel ATV's (Schenbeck 1982).

Statistical Aspects

Small mammals, including nontarget deer mice, were sampled on each of 18 sites one

TABLE 1. Pretreatment and posttreatment relative densities (unique mammals/trap night) of deer mice (*Peromyscus maniculatus*) on zinc phosphide treated and control sites. Adjusted means were estimated as posttreatment minus pretreatment.

Treatment	Relative density ($\bar{x}$ ± SE)			Treatment effect	Significance level (control versus treated)[a]
	Pretreatment (1983)	Posttreatment (1984)	Adjusted means		
IMMEDIATE IMPACTS					
September					
Treated	8.3 ± 2.6	1.3 ± 0.7	−7.0 ± 2.6		
Control	4.3 ± 1.9	2.7 ± 0.9	1.7 ± 1.2	−5.3 ± 2.6[b]	—
POSTTREATMENT IMPACTS					
May					
Treated	8.0 ± 1.5	8.7 ± 0.3	0.7 ± 1.2		
Control	11.0 ± 3.0	12.3 ± 3.3	1.3 ± 3.8	−0.7 ± 2.1	0.878
June					
Treated	7.0 ± 2.1	7.6 ± 0.3	0.7 ± 2.4		
Control	3.7 ± 1.9	10.7 ± 2.6	7.0 ± 4.2	−6.3 ± 1.6	0.253
July					
Treated	3.0 ± 1.2	8.3 ± 2.3	5.3 ± 1.9		
Control	2.0 ± 1.0	10.7 ± 1.7	8.7 ± 1.5	−3.3 ± 1.6	0.223
August					
Treated	8.3 ± 2.6	4.3 ± 0.3	−4.0 ± 2.6		
Control	4.3 ± 1.9	4.7 ± 1.9	0.3 ± 1.9	−4.3 ± 1.0	0.254

[a] Randomization test used to detect differences between pairs of adjusted means, after significant F-protection at $\alpha < .10$.

[b] Treatment effects were not significant (P .295); therefore, statistical significance of contrasts was not determined for September.

week prior to rodenticide application in September 1983 (pretreatment). The fourth day after rodenticides were applied, posttreatment counts were taken on all sites to assess immediate impacts. We evaluated long-term (September 1983 through August 1984) impacts by comparing small mammal data collected during September 1983 with all 1984 trap sessions. Rodenticides were not applied in 1984.

Each rodenticide was evaluated for impacts on nontarget small mammals by comparing the change of mean relative density on each cluster of treated sites with the change observed on respective control sites (Uresk et al. 1988) (Tables 1–3). Five comparisons through time included one for immediate impacts (September 1983), measured between pretreatment and posttreatment (1983) poisoning, and four comparisons that measured differences between pretreatment (1983) and posttreatment (1984) densities. When a significant correlation existed between pretreatment and posttreatment observations, analysis of covariance was used to estimate treatment effect (Deisch 1986, Uresk et al. 1988). Subtraction (Green 1979) was used if the correlation was nonsignificant.

Comparisons between and among rodenticides for impact were produced by forming pairwise contrasts between individual rodenticide treatment effects. Randomization procedures were used to estimate statistical significance of the various contrasts (Edgington 1980, Romesburg 1981, Uresk et al. 1986, Uresk et al. 1988). Rejection of any rodenticide impact (type II error) to nontarget small mammals was considered more serious than potential incorrect acceptance of a significant treatment effect (type I error) (Tacha et al. 1982). After significant ($P = .10$) treatment effects were detected, type II error protection was produced by testing each contrast individually. Type I error protection was afforded by testing for treatment effects with analysis of variance or covariance (Carmer and Swanson 1973).

Individual contrasts were considered biologically significant at $P = .20$. Although an alpha of .20 is not a standard level of significance, it is becoming more accepted for ecological field studies (Hayne 1976) and is used here to protect against missing effects on nontarget species. The number of sites available in this study produced a power of .80. This was an acceptable combination of type I

TABLE 2. Pretreatment and posttreatment relative densities (unique mammals/trap night) of deer mice (*Peromyscus maniculatus*) on strychnine only treated and control sites. Adjusted means were estimated as posttreatment minus pretreatment.

Treatment	Relative density ($\bar{x}$ ± SE)			Treatment effect	Significance level (control versus treated)[a]
	Pretreatment (1983)	Posttreatment (1984)	Adjusted means		
IMMEDIATE IMPACTS					
September					
Treated	0.7 ± 0.7	1.7 ± 1.7	1.0 ± 2.1		
Control	9.0 ± 3.2	6.0 ± 4.0	−3.0 ± 2.0	4.0 ± 2.8[b]	—
POSTTREATMENT IMPACTS					
May					
Treated	5.7 ± 3.0	1.7 ± 1.7	−4.0 ± 2.1		
Control	11.7 ± 1.8	3.0 ± 1.5	−8.7 ± 3.3	4.7 ± 2.1	0.314
June					
Treated	2.7 ± 1.5	0.3 ± 0.3	−2.3 ± 1.5		
Control	13.0 ± 1.2	2.3 ± 1.9	−10.7 ± 2.3	8.3 ± 1.8	0.043
July					
Treated	3.7 ± 2.7	0.3 ± 0.3	−3.3 ± 2.8		
Control	4.3 ± 2.3	1.0 ± 1.0	−3.3 ± 1.7	−0.1 ± 1.6	0.999
August					
Treated	0.7 ± 0.7	0.0 ± 0.0	−0.7 ± 0.7		
Control	9.0 ± 3.2	1.3 ± 1.3	−7.7 ± 2.0	7.0 ± 1.1	0.034

[a] Randomization test used to detect differences between pairs of adjusted means, after significant F-protection at $\alpha < .10$.

[b] Treatment effects were not significant ($P = .295$); therefore, statistical significance of contrasts was not determined for September.

and II error protection (Carmer 1976) and allowed for reasonable biological inferences to be drawn from the data.

RESULTS

Effects of Rodenticides

Eleven small mammal species captured on 18 sites included deer mouse (*Peromyscus maniculatus*), northern grasshopper mouse (*Onychomys leucogaster*), Ord's kangaroo rat (*Dipodomys ordii*), thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*), western harvest mouse (*Reithrodontomys megalotis*), hispid pocket mouse (*Perognathus hispidus*), plains pocket gopher (*Geomys bursarius*), prairie vole (*Microtus ochrogaster*), house mouse (*Mus musculus*), olive-backed pocket mouse (*Perognathus fasciatus*), and Norway rat (*Rattus norvegicus*). Deer mouse was the only species captured in sufficient numbers to statistically evaluate for rodenticide effects.

There were no immediate impacts of any of the three rodenticide treatments ($P = .295$) on deer mouse relative densities in September 1983 (Tables 1–3). However, relative densities of deer mice changed 79% from 5.8 to 1.2 unique animals immediately after application of zinc phosphide (Uresk et al. 1988). Long-term impacts of the three rodenticides were detected.

On zinc phosphide sites, deer mouse densities were not significantly different between control and treated sites, but densities on treated sites were consistently lower compared with control sites (Table 1). On strychnine sites, relative densities of deer mice were significantly higher on treated sites in June ($P = .043$) and August ($P = .034$) (Table 2). Sites with prebaited strychnine showed higher densities on treated sites in August 1984 ($P = .063$) (Table 3).

Comparisons of Three Rodenticides for Impacts

Comparisons of the impacts of the three rodenticides immediately after application showed no differences ($P = .10$) for deer mouse densities in September 1983. Zinc phosphide lowered densities of deer mice more than did strychnine alone in June 1984 ($P = .030$) and August ($P = .018$); in May and July no differences in reduction rates were measured. There were no differences among treatment effects of zinc phosphide compared

TABLE 3. Pretreatment and posttreatment relative densities (unique mammals/trap night) of deer mice (*Peromyscus maniculatus*) on prebaited strychnine treated and control sites. Adjusted means were estimated as posttreatment minus pretreatment.

Treatment	Relative density ($\bar{x}$ ± SE)			Treatment effect	Significance level (control versus treated)[a]
	Pretreatment (1983)	Posttreatment (1984)	Adjusted means		
IMMEDIATE IMPACTS					
September					
Treated	9.3 ± 0.9	4.0 ± 1.2	−5.3 ± 1.9		
Control	16.3 ± 2.7	13.0 ± 5.5	−3.3 ± 3.7	−2.0 ± 2.7[b]	—
POSTTREATMENT IMPACTS					
May					
Treated	17.0 ± 3.1	5.3 ± 0.9	−11.7 ± 2.3		
Control	20.3 ± 3.0	7.7 ± 1.5	−12.7 ± 4.7	1.0 ± 2.1	0.864
June					
Treated	20.7 ± 4.3	0.3 ± 0.3	−20.3 ± 4.5		
Control	21.3 ± 2.2	2.7 ± 2.2	−18.7 ± 4.3	−1.7 ± 1.6	0.795
July					
Treated	10.3 ± 3.0	0.0 ± 0.0	−10.3 ± 3.0		
Control	11.0 ± 3.8	3.0 ± 2.1	−8.0 ± 5.9	−2.3 ± 1.6	0.726
August					
Treated	9.3 ± 0.9	0.7 ± 0.7	−8.7 ± 0.3		
Control	16.3 ± 2.7	0.3 ± 0.3	−16.0 ± 3.0	7.3 ± 1.1	0.063

[a] Randomization test used to detect differences between pairs of adjusted means, after significant F-protection at $\alpha < .10$.

[b] Treatment effects were not significant (*P* .295); therefore, statistical significance of contrasts was not determined for September.

with prebaited strychnine on deer mice from May through July. Impact of zinc phosphide in August ($P = .027$) was greater than that of prebaited strychnine. Comparison of treatment effects between the two strychnine rodenticides indicated that strychnine alone was more effective than prebaited strychnine for lowering densities of deer mice in June ($P = .174$).

DISCUSSION

Of the three rodenticide applications used for prairie dog control, only zinc phosphide consistently lowered deer mouse densities. On these sites zinc phosphide was also most effective in reducing prairie dog burrow activity (Apa 1985). Deer mice consume seeds (Baker 1968, Flake 1973, Sieg et al. 1986) and are susceptible to granular rodenticides. After initial rodenticide treatments, long-term changes in deer mouse populations are associated with habitat changes such as increased density of vegetation (Uresk 1985) because of lack of clipping by prairie dogs. Deer mice are adapted to live in more open habitat (Baker 1968, Jones et al. 1983, MacCracken et al. 1985, Agnew et al. 1986), and their numbers decrease with increased vegetation height and canopy cover. Prairie dog burrows were initially devoid of vegetation before rodenticide application; increased plant canopy cover and aboveground biomass occurred with absence of prairie dogs (Klatt 1971, Potter 1980) and contributed to a decrease in deer mouse densities.

Deer mouse densities were variable over the long-term period with the two strychnine treatments, especially when prebaiting was applied. Deer mouse populations generally increased after treatment with the strychnine only. This increase can be attributed to limited control of the black-tailed prairie dogs (Uresk et al. 1986), which provided and maintained suitable habitat for deer mice (Agnew et al. 1986). Changes in densities of deer mice may also be attributed to seasonal movements of these animals from other areas (Terman 1968) and possible lower predation. An influx of rodents usually occurred in the spring when yearling deer mice established home ranges (MacCracken et al. 1985), and lower densities in August were due to dispersal of young-of-the-year (Falls 1968, Metzgar 1980).

Crabtree (1962) and Marsh et al. (1970) found that zinc phosphide produced a response-stimulating odor that proved attractive to small mammals, but strychnine did not have an attractive effect on rodents. Based on these findings, discontinuation of zinc phosphide for prairie dog control is not recommended or required, but land management plans should include considerations for possible nontarget deer mouse losses. We found that use of strychnine alone or prebaited strychnine generally showed a long-term increase in deer mouse densities. Use of these two strychnine treatments for prairie dog control appears to impose the least threat to nontarget deer mice.

While this study addressed direct effects of rodenticides (zinc phosphide, prebaited strychnine, and strychnine alone) on deer mouse densities, impacts on other nontarget small mammals could not be evaluated because of the small populations observed. We suspect that granivores, such as *Perognathus* spp. and *Dipodomys* spp., found on prairie dog towns in western South Dakota, may also be affected by rodenticides. Further investigations are needed to assess nontarget losses of small mammals other than deer mice.

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ON THE TYPIFICATION OF *OXYTROPIS BOREALIS* DC.

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ABSTRACT.—The status of the name *Oxytropis borealis* DC. is reviewed as it applies to North American plants. A summary of the infraspecific taxa is presented, and several nomenclatural combinations are proposed: *Oxytropis borealis* DC. var. *hudsonica* (Greene) Welsh; *O. borealis* var. *sulphurea* (Pors.) Welsh; *O. borealis* DC. var. *viscida* (Nutt.) Welsh. One new taxon, *Oxytropis borealis* DC. var. *australis* Welsh, is described from Utah and Nevada, USA.

Preparation of a revisionary summary of the genus *Oxytropis* DC. for the Flora North America Project necessitates that nomenclatural changes and new taxa be presented prior to publication in that project. The principal reason for this paper involves the nomenclature of *O. borealis*, a name that has figured in various taxonomic treatments of the genus in North America and elsewhere for more than a century (Barneby 1952, Bunge 1874, Gray 1884, Jurtsev 1986, Torrey and Gray 1838, Vasil'chenko, Fedchenko, and Shishkin 1948). The American phases of *Oxytropis* section *Gloeocephala* have passed under a series of names centering on *Oxytropis viscida* Nutt. ex Torr. & Gray (1838). Since the section *Gloeocephala* has circumboreal or at least amphiberingian representation, American workers were almost certain that there was an older name in the Old World literature. Indeed, Barneby (1952) in his revision of the North American species of *Oxytropis* cited two specific epithets older than that of *O. viscida*. And Boivin (1967), in his attempt at summarizing the Canadian portion of the section, transferred the infraspecific taxa to *O. leucantha* (Pallas) Pers. An examination of the type of that species demonstrated that it lacked glands typical of members of the section *Gloeocephala;* it was indeed a portion of the *O. campestris* (L.) DC. sensu lato (Welsh 1972). The transfers to that entity, thus, are incorrect and are merely nomenclatural baggage that accompanies the genus in perpetuity.

Welsh (1967, 1974) and Welsh et al. (1987) essentially followed the lead of Barneby (1952), who chose a wait-and-see attitude with regard to the earliest name for the North American complex. Examination of the types was necessary prior to a final determination of the question of an earlier name for the North American materials.

Bunge (1874) treated two main sections of glandular oxytropes, *Gloeocephala* and *Polyadenia*. The main diagnostic feature used in segregation of members of these sections is the arrangement of the leaflets—*Gloeocephala* having opposite, subopposite, or scattered leaflets and *Polyadenia* having pseudofaciculate leaflets. Since North American viscid oxytropes have both leaflet arrangements, but mainly opposite, subopposite, or scattered, it is necessary to review the names of Old World representatives of both *Gloeocephala* and *Polyadenia*. The names *O. muricata* (Pallas) DC. (*Phaca muricata* Pallas, Reise 3: 318. 1776) and *O. microphylla* (Pallas) DC. (*Phaca microphylla* Pallas, Reise 3: 744. 1776) were both published prior to the next available name in *Gloeocephala*, i.e., *O. borealis* DC. Authentic (probable type) specimens of these and others of the *Polyadenia* were obtained on loan from the herbarium of the Komarov Botanical Institute herbarium (LE). Neither *O. muricata* nor *O. microphylla* seems to be within the concept of the glandular phases of *O. borealis* with pseudofaciculate leaflets as they occur in North America.

Thus, the earliest name available in section *Gloeocephala* in North America is *O. borealis* DC., which is based on a specimen (Fig. 1) deposited in the Prodromus herbarium at

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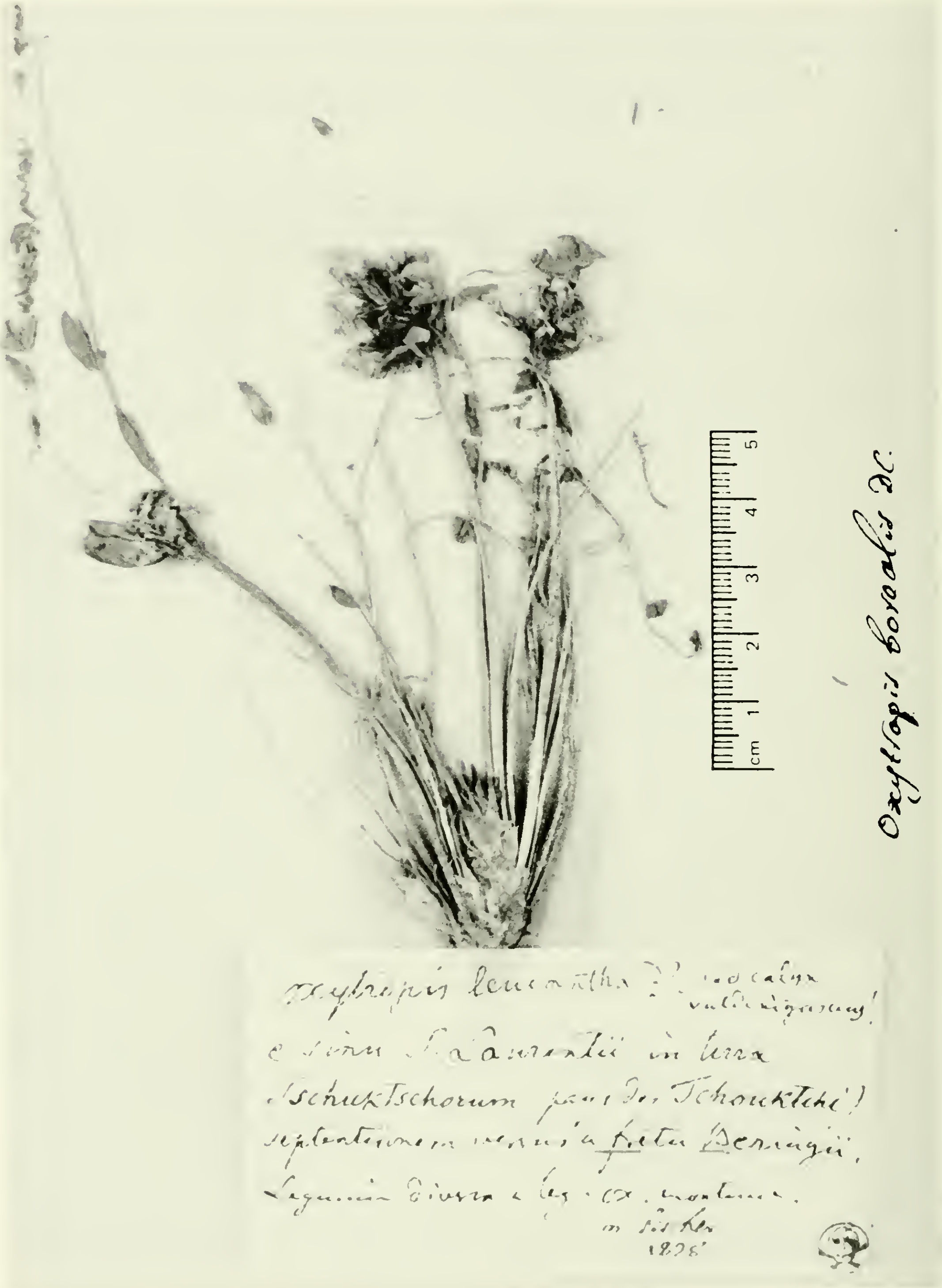
Oxytropis leucantha ?? sed calyx valde nigrescens!
e sinu S. Laurentii in terra
Tschuktschorum (pays des Tchouktchi)
septentrionem versus a freto Beringii.
Legumina diversa a leg. Ox. montana.
m. Fischer
1828
cm 1 2 3 4 5
Oxytropis borealis DC.

Fig. 1. Holotype of *Oxytropis borealis* DC. The specimen is at G-DC.

Geneva. The specimen is in poor, but not terrible, condition, essentially what is expected for many historical types. The specimen appears never to have been in good condition after its collection. The flowers are crumpled as though they had been wet following collection, or even following mounting. The question of glandularity was left unanswered in the description by de Candolle in Prodromus (see below). The need to examine portions of the material was critical as to its nomenclatural importance in North American taxonomy.

Detailed photos and fragments of the specimen were sent for examination through the generosity of Dr. A. Charpin, conservateur at Geneve (G-DC.). Of particular importance among the fragments loaned is a black, hairy bud with calyx teeth still connivent. The teeth are clearly glandular verrucose. Other fragments include a portion of a flower and part of a floral bract. The bract, a very long structure not unlike those of many Alaskan specimens, is definitely dorsally glandular also. The plant size and nature of other features, though shattered, are well within the morphological limits of the group as it occurs in North America. Clearly this material belongs to that portion of the *Gloeocephala* complex treated by Barneby in 1952 as *O. viscida* var. *subsucculenta*. Having priority, the name *O. borealis* must replace *O. viscida* for North American portions of the complex. The author hopes the transfers proposed below are not additional nomenclatural baggage.

Oxytropis borealis DC., Prodr. 2: 275. 1825.

> O. borealis, subacaulis, pilis scaporum stipularumque setosis patulis, petiolorum paucis, foliolis elliptico-lanceolatis subtus glabris superne pilosis scapi folii longitudine, floribus capitatis, bracteis calycis nigro-hispidissimi longitudine. In terra Tschuktschorum ad Sinum Sancti-Laurentii. Stipulae pallidae. (v.s. Comm. a cl. Fisch.) (l.c.).

TYPE LOCALITY.—"In terra Tschuktschorum ad sinum Sancti-Laurentii," collector not stated.

TYPE.—"e sinu S. Laurentii in terra Tschuktschorum (pays des Tchouktchi) septentrionem versus a fretu Beringii. Legumina diversa a leg. ox. montana. m. [Messien] Fischer 1825" G-DC.!. The specimen cited above is the only one bearing the name *O. borealis* in the Prodromus herbarium, and it is regarded as the holotype (Fig. 1).

The species, as it occurs in North America, consists of a series of mainly intergrading varieties as indicated below. They differ in compactness of inflorescence, size of flowers, length of floral bracts, and other features that tend to grade individually and collectively into each other. As intergradation occurs, the taxa within the *boreale* complex match those of infraspecific taxa in other specific complexes in this genus.

Presented below is a summary of the infraspecific taxa as they occur in North America. The writer has examined herbarium materials from all regions of distribution in the continent. Additionally, he has examined the species in the field from the arctic regions of Alaska, Yukon, and Northwest Territories south to its southern limits in Utah and Nevada. Variation is huge in the species as a whole and in the infraspecific taxa. The group has received several interpretations in the past and will undoubtedly be interpreted differently in the future.

Oxytropis borealis DC. var. *borealis*

Distribution: N.W.T. and Alaska; Chukotsk.

Oxytropis uralensis β *subsucculenta* Hook., Fl. Bor.-Amer. 1: 146. 1831. *Oxytropis viscida* var. *subsucculenta* (Hook.) Barneby, Proc. Calif. Acad. IV, 27: 246. 1952. Type: "Arctic seashore, to the east of the Mackenzie River," Dr. Richardson s.n.; holotype K.

Oxytropis borealis β Hook. & Arnott, Bot. Beechey Bot. 122. 1832.

Oxytropis campestris var. *verrucosa* Ledebour, Fl. Ross. 1: 591. 1842. Type: "in terra Tschuktschorum ad sinum Sancti-Laurentii," the collector not stated.

The relatively few leaflets, ample flowers, and condensed, copiously hirsute inflorescence in combination allow this entity to be rather readily identified. It consists, at least in part, of what has passed under the name of *O. glutinosa* Pors., who excluded the type of "*subsucculenta*" from consideration in treatment of the genus in "Vascular Plants of Continental Northwest Territories, Canada" (Porsild and Cody 1980). Included within the concept of var. *borealis* is the *O. uralensis* β *subsucculenta* Hook., the basis of *O. viscida* var. *subsucculenta* (Hook.) Barneby.

Oxytropis borealis var. *hudsonica* (Greene) Welsh, comb. nov.

Aragallus hudsonicus Greene, Proc. Biol. Soc. Wash. 18: 17. 1905. *Oxytropis viscida* var. *hudsonica* (Greene) Barneby, Proc. Calif. Acad. IV, 27: 245.

1952. *O. viscida* ssp. *hudsonica* (Greene) Love & Love, Taxon 31: 347. 1982. *O. leucantha* var. *hudsonica* (Greene) Boivin, Naturaliste Canad. 94: 76. 1967. Type: Whale River, Hudson Bay; A. P. Low 14272, 24 June 1896; holotype NDG!.

Oxytropis leucantha var. *hudsonica* f. *galactantha* Boivin, Naturaliste Canad. 94: 76. 1967. Type: Canada: Franklin District, Melville Peninsula, Repulse Bay, along Nauja River, 27 July 1950, P. F. Bruggeman 52; holotype DAO!.

Oxytropis leucantha var. *leuchippiana* Boivin, Naturaliste Canad. 94: 76. 1967. Type: Yukon: Whitehorse, airport area, steep slope, flowers varying in color from yellow to purple, abundant, Gillette & Calder 3181; lectotype here selected DAO!.

This is the phase of the species that occurs in North America mainly east of the Yukon, but with some representation in that province, where it is transitional with both var. *viscida* and var. *sulphurea*. The main diagnostic feature involves the short calyx teeth.

Oxytropis borealis var. *sulphurea* (Pors.) Welsh, comb. nov.

O. viscidula ssp. *sulphurea* Pors., Bull. Nat. Mus. Canad. 121: 247. 1951. Type: Yukon, Rose-Lapie Pass, shaly cliffs by waterfall E of Lapie Lake, mile 105 [Canol Road], Pors. & Breitung 10198, 19 July 1944; holotype CAN; isotypes ISC!, S!.

Oxytropis sheldonensis Pors., Bull. Nat. Mus. Canad. 121: 246. 1951. Type: Mount Sheldon, on rocky granite ledges at or near the summit, opposite mile 122 [Canol Road], Pors. & Breitung 11750, 11 August 1944; holotype CAN!; isotypes ISC!, US!.

Oxytropis verruculosa Pors., Bull. Nat. Mus. Canad. 121: 246, 1951. Type: Yukon: Rose-Lapie Pass, rocky ledges on dry slope W of mile 116 [Canol Road], Pors. 10072, 1944; holotype CAN!; isotype S!.

These are the pallid-flowered plants of the Yukon and Alaska. In their most typical condition the racemes are compactly and uniformly small flowered. They vary from that norm to elongate racemes with small to large flowers. The bracts are mainly small, but in some they are very long and conspicuous in the inflorescence. On the one side the plants seem to grade with var. *hudsonica* and on the other with both var. *viscida* and var. *borealis*.

Oxytropis borealis var. *viscida* (Nutt.) Welsh, comb. nov.

Oxytropis viscida Nutt., ex Torr. & Gray, Flora N. Amer. 1: 341. 1838. *Aragallus viscidus* (Nutt.) Greene, Pittonia 3: 211. 1897. *Astragalus viscidus* (Nutt.) Tidestrom, Proc. Biol. Soc. Wash. 50: 19. 1937. *O. campestris* var. *viscida* (Nutt.) S. Watson, U.S. Geol. Expl. 40th Parallel, Bot. 5: 55. 1871. *Spiesia viscida* (Nutt.) Kuntze, Rev. Gen. 206. 1891. *O. leucantha* var. *viscida* (Nutt.) Boivin, Naturaliste Canad. 94: 77. 1967. Type: Rocky Mountains, near the sources of the Oregon [SW Wyoming], Nuttall s.n. 1834; syntypes NY!, PH.

Aragallus viscidulus Rydb., Mem. N.Y. Bot. Gard. 1: 253. 1900. *O. viscidula* (Rydb.) Tidestrom, Contr. U.S. Nat. Herb. 25: 332. 1925. Type: Montana, Melrose, Silver Bow County, Rydberg 2716; holotype NY! (type specified by Barneby 1952).

Aragallus viscidula var. *depressus* Rydb., Mem. N.Y. Bot. Gard. 1: 523. 1900. *Oxytropis leucantha* var. *depressa* (Rydb.) Boivin, Naturaliste Canad. 94: 77. 1967. Type: Haystack Mt., Stillwater County, Montana, Tweedy 120; holotype NY!.

Oxytropis gaspensis Fern. & Kelsey, Rhodora 30: 123. 1928. *Astragalus gaspensis* (Fern. & Kelsey) Tidestrom, Proc. Biol. Soc. Wash. 50: 19. 1937. *O. leucantha* var. *gaspensis* (Fern. & Kelsey) Boivin, Naturaliste Canad. 94: 76. 1967. Type: Quebec, Mont St. Pierre, Gaspe County, Fernald & Smith 25874, 14 August 1933; holotype GH; isotypes CAS!, NY!.

Oxytropis ixodes Butters & Abbe, Rhodora 45: 2, tab. 745, figs. 1–6. 1943. *O. leucantha* var. *ixodes* (Butters & Abbe) Boivin, Naturaliste Canad. 94: 76. 1967. Type: Minnesota, South Fowl Lake, Cook County, Butters, Abbe, & Burns 611, 27 June 1940; holotype MINN; isotypes GH, NY!, PH!, US!.

Oxytropis leucantha var. *magnifica* Boivin, Naturaliste Canad. 94: 77. 1967. Type: Alberta, Macloed, High River, 27 June 1902, J. Fletcher s. n.; holotype DAO!.

Oxytropis ixodes var. *ecaudata* Butters & Abbe, Rhodora 45: 4. 1943. Type: Ontario, Thunder Bay District, Butters, Abbe, & Burns 682; holotype MINN.

DISTRIBUTION.—Alaska, Yukon, N.W.T., Quebec, British Columbia, Alberta, Minnesota, Oregon, Idaho, Wyoming, Nevada, Utah, Colorado, and California.

This variety includes almost as much diversity as the species as a whole. The numerous subunits are held together by tenuous characteristics that are difficult to define or place in a key. Variation is often great in subpopulations from adjacent hillsides or even on a single gravel bar, especially in the arctic. One is reminded of the conditions of morphological variation occurring in the boreal *O. nigrescens* var. *nigrescens*, as regarded by this author. Unless one is willing to support a taxonomy wherein the purported taxa are largely sympatric and consist of morphological subunits whose genetic continuity is questionable, made up of a series of similar plants held together by that similarity and not by genetic linkage, there seems to be no reasonable way to segregate the morphological variants as taxa. The rather large number of synonyms, often at specific or varietal levels, reflects the attempts at segregation.

Oxytropis borealis var. *australis* Welsh, var. nov.

Similis *O. boreali* var. *viscida* (Nutt.) Welsh sed in floribus pallidis et inflorescentia vulgo foliis saepe subaequalis distinguitur.

Caespitose, acaulescent, 6–19 cm tall; pubescence basifixed; stipules glabrous to glandular or sparingly so; leaves 4–15.5 cm long; leaflets 15–33, 1.5–20 mm long, 1–5 mm wide, oblong to lanceolate or elliptic, sparingly pilose to glabrate or glabrous on both sides, sometimes also glandular; scapes 2–16.5 cm long, spreading-hairy; racemes 2- to 11-flowered, the flowers spreading-ascending, the axis 1–3 cm long in fruit; bracts glabrous dorsally, glandular; flowers 11–19 mm long, whitish or rarely suffused with pink; calyx 5–11 mm long, the shortly cylindric tube 4–7 mm long, the teeth 1.5–3.5 mm long, triangular-subulate, commonly glandular; pods erect, sessile, ovoid to subcylindric, 8–16 mm long, 4–6 mm thick, glandular.

DISTRIBUTION.—Utah and Nevada, USA.

TYPE.—Utah: Sevier Co., open hillside, E of Hogan Pass, along Utah Hwy 72, at 8300 ft. elevation. Flowers white. T25S, R4E, 23 July 1967, S. L. Welsh, D. Isely, & G. Moore 6452; holotype BRY!, isotype ISC!, NY! (a total of 17 duplicates distributed earlier as *O. viscida* Nutt.). Other collections: Utah: Emery Co., 10 km due W of Ferron, 2 June 1977, E. Neese & S. White 3022; do, E end of Bald Ridge, T16S, R8E, S10, 11 July 1979, R. Foster. Sanpete Co., 20 km up Ferron Canyon, T19S, R5E, S36, 9 June 1977, S. Clark & K. Taylor 2473; do, Ferron Mt., T20S, R5E, S33, 11 July 1989, M. A. Franklin 6794. Sevier Co., Aspen Spring, Salina Canyon, 18 June 1943, W. P. Cottam 9191; do, 1 km SE of Mt. Hilgard, 25 August 1965, R. Stevens 110; do, Desert View, ca 1.5 km S of Hogan Pass, ca 23 km N of Fremont, T25S, R4W, 10 May 1969, S. L. Welsh, D. Atwood, L. Higgins 8971; do, 21 km due SSW of Fremont Jct., T26S, R4E, S4, 8 July 1977, S. L. Welsh 15359; do, head of Clear Creek below Hilgard Mt., T24S, R4E, S26, 30 June 1977, S. Clark 2662; do, Clear Creek ca 3 km SE of Clear Creek Guard Station, T24S, R4E, 10 June 1981, D. Atwood 7947; do, milepost 18 on Utah Hwy 72, T25S, R4E, S22, 31 May 1986, R. Kass, E. Neese, B. Neely 2345; do, milepost 18 on Utah Hwy 72, T26S, R4E, S4, 31 May 1986, E. Neese, B. Neely, R. Kass 17521; do, ca 13 km N of Fish Lake, T24S, R3E, S33, 25 July 1987, B. Franklin & J. & J. Chandler 4999. Wayne Co., Elk Horn Guard Station, T27S, R4E, S15, 17 June 1977, S. Welsh 14982; do, Paradise Valley, T25S, R4E, 24 July 1978, D. Atwood 6922; do, Elkhorn Campground, T24S, R4E, S15, 16 June 1986, J. M. Porter 3918; do, on the slopes overlooking Deep Creek, T27N, R4E, S25, 17 June 1986, J. M. Porter 3863. Nevada: Elko Co., Ruby Mountains, S of Harrison Pass, T28N, R57E, ca S25, 7 August 1967, J. L. Gentry & G. Davidse 1823. Nye Co., Toquima Range, Pine Creek drainage, T11N, R45E, 24 July 1964, J. L. Reveal 657; do, Toquima Mts. ca 110 km S of Austin, T11N, R45E, ca S28, 15 July 1973, A. Cronquist 11048; do, Toquima Range, Mt. Jefferson, head of South Fork Pine Creek, T11N, R45E, S29 & S32, 18 July 1978, K. R. Genz 8246; do, north side of Timber Mountain, Grant Range, T6N, R57E, 27 June 1979, M. J. Williams & A. Tiehm 79-109-4.

This southern phase of *O. borealis*, though mainly montane in distribution, occurs mostly on xeric sites in sagebrush, black sagebrush, grass, ponderosa pine, and aspen parkland communities, often on exposed ridges or outcrops. Main substrate types are of igneous origin, either granitic- or basaltic-derived soils, but limestone also serves as a substrate. Elevational range varies from 2135 to 3355 m.

The differences cited in the diagnosis are not absolute, as is usual for infraspecific and even specific taxa in this genus. Flower color is typically white or ochroleucous, but some are occasionally tinged with pink; and some that appear to be white when fresh fade slightly lavender on drying. Inflorescences tend to be only slightly longer than the leaves, or even slightly shorter, but some have inflorescences much surpassing what appear to be juvenile leaves with tiny leaflets. The herbage is often conspicuously glandular, with sand grains and plant fragments adhering. The stipules are occasionally quite glandless, however. In spite of the variation in morphology, these plants appear to represent a xeric southern phase related to the typically more mesic var. *viscida*. That variety, shorn of var. *australis*, is not much less polymorphic. There are individual plants, and possibly even subpopulations, within var. *viscida* that simulate var. *australis.* Plants from the Wallowa Mountains of northeastern Oregon are almost as variable as var. *viscida* as a whole.

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REPRODUCTION OF THREE SPECIES OF POCKET MICE (*PEROGNATHUS*) IN THE BONNEVILLE BASIN, UTAH

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ABSTRACT.—Data on reproduction of three species of pocket mice (*Perognathus*) occurring in northern Utah are summarized. *Perognathus parvus* and *P. formosus* bred in spring but not the remainder of the year. This occurred despite mild fall and winter temperatures and shallow snowcover. Litter sizes for *P. parvus* and *P. formosus* were similar to those reported by previous investigators. A small sample of *P. longimembris* indicated they may have much larger litters (averaging 5.78 young) than previously reported for laboratory populations. Adult body mass was positively correlated with testis mass in all species, and with litter size in *P. parvus*.

Pocket mice (genus *Perognathus*) are widespread and ubiquitous components of rodent communities in western North America. Despite a growing body of knowledge concerning their ecology, such as competitive interactions (e.g., Brown and Lieberman 1973), seed-caching (e.g., Kenagy 1973, Reichman 1975), and physiological adaptations to arid environments (MacMillen 1972), studies of pocket mouse reproduction are primarily anecdotal or based on laboratory colonies (Jones 1985).

Here we report on reproduction in field populations of the long-tailed pocket mouse (*Perognathus formosus*), Great Basin pocket mouse (*P. parvus*), and little pocket mouse (*P. longimembris*) in the Bonneville Basin of northwestern Utah. Specifically, we examine seasonal variation in reproductive activity, litter size, and allometric relationships between body mass and reproductive variables.

STUDY AREAS

Most *P. formosus* were trapped on the north end of the Newfoundland Mountains ($N = 161$), with a few specimens from the Grassy Mountains ($N = 24$) and Floating Island ($N = 12$). *P. parvus* were collected primarily from the Grassy Mountains ($N = 21$), Hogup Mountains ($N = 36$), and Stansbury Island ($N = 32$). *P. longimembris* in this study were sampled from Floating Island ($N = 16$), located 30 miles NE of Wendover (Tooele County), Utah, in the Bonneville Salt Flats. Collection sites are between 1300 and 1420 m in elevation on the Floating Island, Newfoundland Mountain, and Stansbury Island sites; and 1650 m in the Hogup Mountain and Grassy Mountain sites (Fig. 1).

All collection sites are dominated by northern cold-desert vegetation, including sagebrush (*Artemisia* spp.), saltbush (*Atriplex* spp.), rabbitbrush (*Chrysothamnus* spp.), horsebrush (*Tetradymia* spp.), greasewood (*Sarcobatus* spp.), and juniper (*Juniperus osteosperma*). The dominant shrubs vary according to elevational, moisture, and soil salinity gradients. All sites show a high degree of similarity in plant genera (39–52% overlap, using Jaccard's index of similarity) with the exception of Stansbury Island, which ranges between 22% and 29% similarity when paired with other sites. This is probably due to the increased diversity found in dunes sampled on the north shore of this island.

METHODS

Specimens were live-trapped or snap-trapped on a monthly basis in 1986 on the Newfoundland and Grassy mountains for approximately 500 trap nights per month. Pocket mice from Stansbury Island and Floating Island were sampled between April and September.

Mice were euthanized and frozen on dry ice in the field. In the laboratory, mice were

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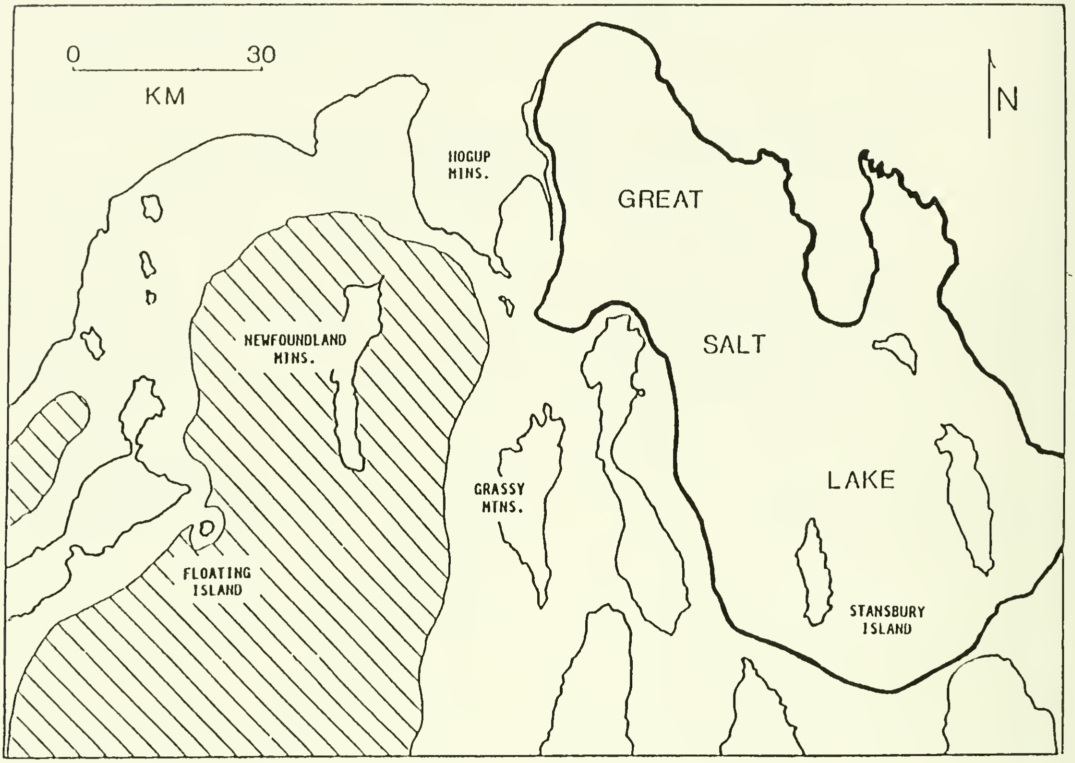

Fig. 1. Study areas in northwestern Utah sampled for three species of *Perognathus*. Area in hatchmarks indicates the extent of barren salt flats. Contour lines are drawn at approximately 1300 m.

weighed to the nearest 0.5 g and measured (total length, tail, hind foot, ear) to the nearest millimeter. Reproductive tracts were removed and placed in alcohol/formalin/acetic acid (AFA) mixture (90 parts 70% ethanol, 5 parts each formalin and glacial acetic acid). Histological procedures followed those of Brown (1964) and Duke (1957).

Testes were stripped of the epididymides and measured lengthwise to the nearest 0.1 mm using an ocular micrometer. Testes were then dried at 80 C for 48 h and weighed to the nearest 0.1 mg on a Mettler AE160 electronic analytical balance.

Uteri and ovaries were cleared through an alcohol-xylene series using Hemo-De, a xylene substitute. Placental scars were counted at this stage and ovaries infiltrated and embedded in paraffin for sectioning. Serial sections 10 microns thick of the entire ovary were stained in Gill's hematoxylin and mounted with Permount mounting medium. Corpora lutea were counted on a dissecting microscope at 25X magnification. Embryos present were counted and measured to the nearest 1 mm.

RESULTS

Results are based on data from 104 female and 93 male *P. formosus*, 25 female and 64 male *P. parvus*, and 9 female and 7 male *P. longimembris*. All data were taken from individuals in adult pelage. The 1986 field season was divided into three seasons as follows: emergence to late June, July through mid-September, and mid-September through early December. This was done to divide the aboveground activity of the heteromyids into three time lengths of equal sampling intensity.

LONG-TAILED POCKET MICE.—Males were first captured in early March, females in mid-April, and neither showed evidence of breeding at that time. Twenty-nine percent of the females sampled ($N = 17$) through the end of

TABLE 1. Seasonal variation of testis mass (dry weight, mg) and seminal vesicle length (mm) of *Perognathus formosus*.

Season	April–June	July–mid-Sept.	Sept.–Dec.
Testis	158.68 (±5.73) $N = 22$	25.25 (±2.41) $N = 57$	27.28 (±1.81) $N = 11$
Seminal vesicle	8.80 (±0.40) $N = 20$	4.76 (±0.20) $N = 17$	No data*

*No animals with seminal vesicles developed.

TABLE 2. Correlations of body mass with male reproductive variables in three species of *Perognathus*.

Species		*formosus*	*parvus*	*longimembris*
Testis mass	rho (*N*)	.502 (90)	.702 (64)	.618 (7)
	P	<.001	<.001	.139
Seminal vesicle length	rho (*N*)	−.167 (37)	.672 (49)	.314 (6)
	P	.324	<.001	.545

June had corpora lutea. This dropped to only 6.3% ($N = 63$) for July–September (Fisher's Exact test, $X^2 = 7.04$, $P = .018$), and none captured after mid-September showed any signs of reproductive activity. Ten percent of the females ($N = 19$) carried embryos early in the season through June, whereas only 1.3% ($N = 79$) carried embryos in the summer (Fisher's Exact test, $X^2 = 4.38$, $P = .095$).

Male reproductive activity paralleled the observations for females. Testis mass and seminal vesicle lengths were smaller as the season progressed (Table 1), reflecting a spring (April–June) breeding peak followed by breeding inactivity the remainder of the year. Mean testis mass was more than five times greater in the spring than in either summer or fall (Kruskal-Wallis, $X^2 = 50.9$, $P < .001$). Seminal vesicles were nearly twice as long in spring (8.8 mm) as in fall (4.8 mm), reflecting a similar pattern (Mann-Whitney $U = 2.5$, $P < .001$). Adult male body mass was significantly correlated with testis mass (Spearman's rho = 0.502, $P < .001$, $N = 90$, Table 2).

The mean litter size estimated from 35 females with one set of placental scars was 5.89 (±0.30). Nine sets of corpora lutea from separate individuals revealed a smaller estimate of 4.78 (±0.74). Our small sample sizes for these data may reflect the fact that corpora lutea in *Perognathus* regress rapidly (Duke 1957) compared with other species where they may persist for months (Brown and Conaway 1964). Three females with embryos had litters of six, six, and five. Thirty-four percent of the females with placental scars had given birth to more than one litter. No evidence of resorbing embryos or polyovuly was observed.

GREAT BASIN POCKET MICE.—This species also apparently has only one peak breeding effort in the spring, although sample sizes are too small to permit meaningful statistical tests. Males were first captured in mid-April, females about two weeks later. Females were reproductively active (corpora lutea or embryos present) when first captured. Forty-five percent (9 of 20) of females captured had corpora lutea, and 28% (7 of 25) were carrying embryos.

Males caught between April and June had significantly larger testes and seminal vesicles (Table 3) than individuals from the remainder of the season (Mann-Whitney $U = 28.0$, $P < .001$ for testes mass; $U = 46.5$, $P < .001$ for seminal vesicle lengths). Adult male body mass was significantly correlated with testis mass (Spearman's rho = 0.702, $P < .001$, $N = 64$) and seminal vesicle length (Spearman's rho = 0.672, $P < .001$, $N = 49$) (Table 2).

Litter size in this species was approximately five, although this was from a sample of only nine females. One set of placental scars numbered five, seven pregnant females averaged 5.17 (±0.46) embryos, and nine sets of corpora lutea averaged 5.33 (±0.37). No evidence of polyovuly or resorption of embryos was observed. Size of the mother was correlated with the number of corpora lutea (Spearman's rho = 0.738, $P = .023$, $N = 9$) and

Table 3. Seasonal variation of testis mass (dry weight, mg) and seminal vesicle length (mm) of *Perognathus parvus*.

Season	April–June	July–Dec.
Testis	153.09 (±6.54) $N = 22$	61.33 (±5.63) $N = 42$
Seminal vesicle	10.50 (±0.36) $N = 22$	6.77 (±0.39) $N = 27$

embryos (Spearman's rho = 0.611, $P = .145$, $N = 7$). Although based on an extremely small sample, this agrees with correlations found in *Peromyscus maniculatus* (Myers and Master 1983, Cramer 1988).

Little pocket mice.—Litter size averaged 5.78 (±0.22) embryos per litter ($N = 9$). The modal size was six, but most of these were in very early stages of development where uterine swellings were less than 3 mm. One female captured later in pregnancy (crown-rump length of embryos 10 mm) had resorbed one embryo, leaving a potential litter of five. Some preimplantation loss was also noted. Two of the litters of six resulted from seven ova as inferred from corpora lutea counts.

Discussion

Long-tailed pocket mice.—Previous published reports on reproduction in *P. formosus* are few but generally support our findings. For a population in southeastern Washington, French et al. (1974) reported an average litter size of 5.6 (77 litters) and a mean corpora lutea count of 6.0 ($N = 51$), both comparable to the present results. The high proportion of long-tailed pocket mice with placental scars from multiple litters may simply reflect the longevity of this species, which has been estimated as up to four years in mark-recapture studies (French et al. 1974).

The only information on the length of the breeding season for this species was offered by Hall (1946), who found embryos in only 2 of 91 females captured in July in Nevada. Our data on male and female reproductive activity indicating a spring peak and cessation of breeding activity by early July support those observations. Even given a combination of apparently favorable weather conditions in fall and winter, no breeding occurred during this period in long-tailed pocket mice. September and October had above average rainfall (196% and 155% above normal, respectively) but cooler than average temperatures (2.6 and 1.1 C below normal). November and December had below average precipitation (snowcover) (39% and 15% of normal, respectively), and November was 0.9 C warmer than normal (NOAA Climatological Data Annual Summary, Utah 1986). *Peromyscus maniculatus* in the same area continued to breed into December (Cramer 1988). These data suggest that reproductive activity in the fall in these species of pocket mice may be more closely tied to photoperiod than to climatic factors. Reichman and Van De Graaff (1975) showed the onset of reproduction in *Dipodomys merriami* to be dependent on winter rainfall and subsequent spring production of annual seeds and green vegetation. Kenagy and Bartholomew (1981) reported a similar effect of green vegetation on male reproductive development in *Perognathus formosus*. It is possible, then, that habitat productivity cues are important for the onset of breeding in the spring, but cessation of breeding in the fall is dependent on photoperiod.

Great Basin pocket mice.—In a Washington population of Great Basin pocket mice, Scheffer (1938) found an average litter size of 5.16 ($N = 77$) from embryo counts and estimated that few individuals produced more than one litter per year. Iverson (1967) reported a mean litter size of 4.85 ($N = 39$) for a population of *P. parvus* in south central British Columbia. He also found that females bred from April to August and that males were reproductively inactive by mid-August. O'Farrell et al. (1975) also suggested that an average of 1.1 litters per year was produced by this species in south central Washington. Our data support previous estimates of litter size in this species and confirm indirectly the supposition that only one litter per year is produced on average, since we found only a short spring breeding peak. Reproductive activity in both males and females supports the hypothesis of a single spring breeding peak with young-of-the-year deferring reproduction until the following spring.

Little pocket mice.—This species produced an average of four young ($N = 52$) in the laboratory, with a range of one to six (Hayden et al. 1966). Other than Hayden's study, data for this species are scarce. Duke's (1957) study does not specify litter sizes for the three species he studied (same three as in this study), but he cited an average litter size for all three species of 5.38. In our samples, the modal litter size for *P. longimembris* is six, much higher than the average of four reported in the laboratory (Hayden et al. 1966).

Our results suggest that pocket mice in northern Utah generally breed only in the spring although they may produce more than one litter per year. Long-tailed pocket mice and little pocket mice usually have six young per litter, while Great Basin pocket mice usually produce about five young per litter. These data are consistent with previous literature with the exception of our litter estimates for little pocket mice. Even given our relatively small sample sizes, the large discrepancy (two young per litter) between our field data and previous lab estimates (Hayden et al. 1966) suggests that caution be exercised in extrapolating from the lab to the field. This could be particularly misleading when drawing inferences from large literature reviews of diverse data sets (e.g., Jones 1985).

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ECTOMYCORRHIZAL FORMATION BY *PISOLITHUS TINCTORIUS* ON *QUERCUS GAMBELII* × *QUERCUS TURBINELLA* HYBRID IN AN ACIDIC SIERRA NEVADA MINESOIL

R. F. Walker[1]

Recent reports (Walker 1989, 1990) disclosed *Pisolithus tinctorius* (Pers.) Coker & Couch occurring in ectomycorrhizal association with Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), Sierra lodgepole pine (*P. contorta* var. *murrayana* [Grev. & Balf.] Engelm.), and California white fir (*Abies concolor* var. *lowiana* [Gord.] Lemm.) on spoils of the Leviathan Mine in Alpine County, California. This Gasteromycete, which has a near worldwide distribution in temperate, subtropical, and tropical latitudes, is a mycobiont of numerous conifer and hardwood hosts (Marx 1977). In the United States it has been most often observed in association with various pine species on harsh sites in the East, South, and Midwest (Lampky and Peterson 1963, Schramm 1966, Hile and Hennen 1969, Lampky and Lampky 1973, Marx 1975, Medve et al. 1977). Subsequently, *P. tinctorius* has been the focus of concerted efforts to develop pure culture inoculation techniques for nursery-grown pine seedlings (Marx et al. 1976, 1984, 1989a, 1989b). Outplanting trials on southern Appalachian surface mines have demonstrated the potential benefits of planting inoculated seedlings on marginal sites, which include improved survival and growth attributable to enhanced uptake of nutrients (Marx and Artman 1979) and water (Walker et al. 1989). Currently, research is concentrated on identification of potential new host species and sources of locally adapted *P. tinctorius* isolates, as well as improvement of inoculation methods. The findings reported here result from efforts to ascertain the host range of this fungus in the Sierra Nevada and Great Basin.

Leviathan Mine, an inactive, open-pit sulfur mine of approximately 100 ha, is located on the eastern slope of the central Sierra Nevada (38°42′30″N, 119°39′15″W) at an elevation of 2,200 m and receives an average annual precipitation of 50 cm, primarily as snowfall. A comprehensive evaluation of the chemical properties of the minesoil (Butterfield and Tueller 1980) revealed a pH of 4.0–4.5, a deficiency of plant-available N, and a potentially phytotoxic Al concentration. Efforts to revegetate the mine since its closure in 1962 have met with limited success, although more recent attempts using a variety of native and nonnative woody species have been somewhat encouraging. Additionally, the periphery of the mine has been recolonized by several species from the adjoining undisturbed forest, primarily Jeffrey and Sierra lodgepole pine and California white fir. Overall, however, much of the site is either sparsely vegetated or barren.

Further examination of Leviathan Mine spoils in September of 1989 and 1990 revealed *P. tinctorius* in ectomycorrhizal association with seedlings of the hybrid Gambel oak (*Quercus gambelii* Nutt.) × turbinella oak (*Q. turbinella* Greene). These seedlings were planted in 1987 as containerized stock grown from acorns collected in southern Nevada, the only location in the state where this hybrid occurs naturally (Tucker et al. 1961). One to three *P. tinctorius* basidiocarps, dark yellow to brown in color and matching the description of Coker and Couch (1928), were observed near solitary seedlings (Fig. 1A), while numerous basidiocarps were often interspersed among clusters of seedlings. Stipitate, substipitate, and sessile forms were encountered, varying in size from 3 to 6 cm in

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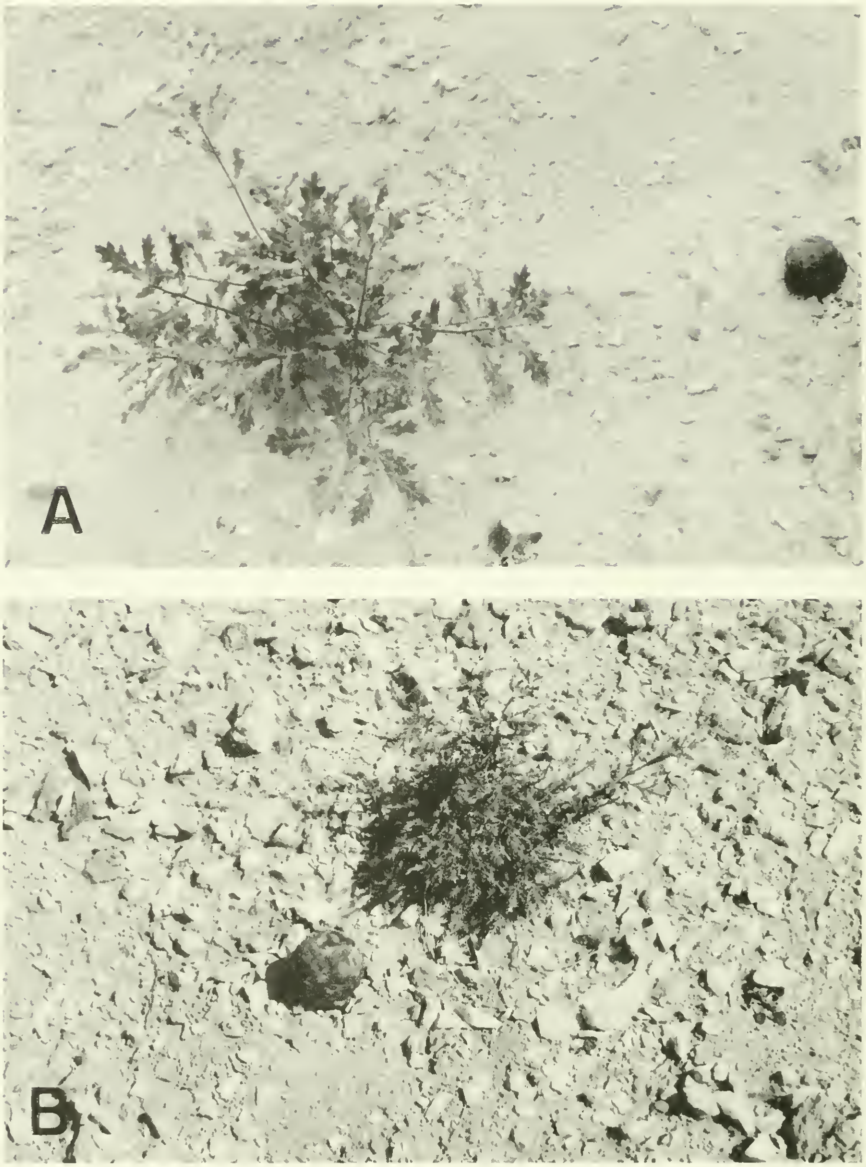

Fig. 1. *Pisolithus tinctorius* basidiocarps on spoils of the Leviathan Mine in Alpine County, California, associated with: A, Gambel oak × turbinella oak hybrid; B, Rocky Mountain juniper.

diameter and from 8 to 15 cm in length; the basidiocarps were rarely more than one meter from the host. Mycelial strands with the characteristic gold-yellow pigmentation of *P. tinctorius* (Schramm 1966) were traced through the minesoil from basidiocarps to seedling root systems, which exhibited the similarly pigmented monopodial, bifurcate, and coralloid ectomycorrhizae formed by this mycobiont (Marx and Bryan 1975a). Excavation of a single representative oak root system revealed that approximately 20% of the lateral roots bore *P. tinctorius* mycorrhizae or an obvious fungal mantle.

Additional *P. tinctorius* basidiocarps were observed in the immediate vicinity of seedlings of Rocky Mountain juniper (*Juniperus scopulorum* Sarg.), Woods rose (*Rosa woodsii* Lindl. var. *ultramontana* [Wats.] Jeps.), and Siberian peashrub (*Caragana arborescens*

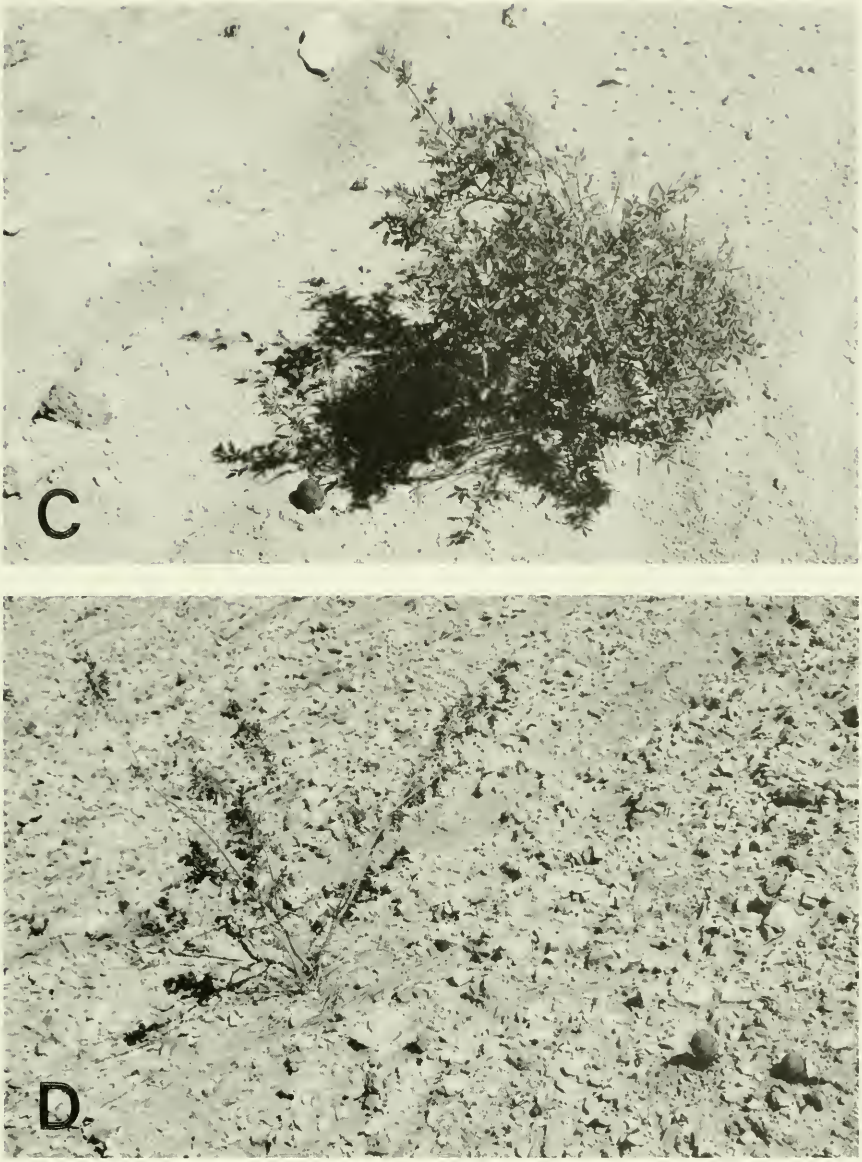

Fig. 1 continued. *Pisolithus tinctorius* basidiocarps on spoils of the Leviathan Mine in Alpine County, California, associated with: C, Woods rose; and D, Siberian peashrub.

Lam.). These three species were also planted as containerized stock with the plantings of Rocky Mountain juniper in 1984 and Woods rose and Siberian peashrub in 1986. Typically, one or two basidiocarps, similar in appearance and size to those found with the hybrid oaks, were again observed within one meter of isolated seedlings of the three species (Figs. 1B-D), and *P. tinctorius* mycelial strands were also traced through the minesoil from the basidiocarps to the root systems. However, no ectomycorrhizae were found on any of these three species following excavation of complete root systems, although species within the genera *Juniperus* and *Rosa* are known to form ectomycorrhizal relationships (Harley and Smith 1983). Rather, on the juniper, rose, and peashrub observed here, only a loose fungal mantle of the characteristic gold-yellow *P. tinctorius* hyphae was apparent on the fine roots. Given that excavated seedling specimens and the associated basidiocarps were ≥ 10 m from any other vegetation, it is likely the fungus derived its requisite carbohydrates solely from these seedlings, as most ectomycorrhizal fungi are assumed to rely on the carbohydrates obtained through the infection of an autotrophic host for completion of their life cycles and subsequent fruiting body production (Marx and Bryan 1975b). Thus, the apparent lack of ectomycorrhizal formation on the juniper, rose, and peashrub may indicate the development of a parasitic, or perhaps ectendomycorrhizal, relationship between *P. tinctorius* and these hosts in the Leviathan Mine, although there are no reports of this fungus forming either of these relationships with any of its previously identified host species.

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NATURAL HYBRID BETWEEN THE GREAT PLAINS TOAD (*BUFO COGNATUS*) AND THE RED-SPOTTED TOAD (*BUFO PUNCTATUS*) FROM CENTRAL ARIZONA

Brian K. Sullivan[1]

Hybridization among toads of the genus *Bufo* is well known (Sullivan 1986). In the southwestern United States hybridization has been documented within both the *americanus* and *punctatus* species groups (Ferguson and Lowe 1969, Sullivan 1986). However, natural hybridization between members of more distantly related species groups is relatively rare. Natural hybrids between *Bufo punctatus* and both *B. boreas* (Feder 1978) and *B. woodhousii* (McCoy et al. 1967) have been described. Documentation of hybridization is important because it provides information about the genetic relatedness of taxa, as well as potential insights into proximate aspects of species recognition and reproductive behavior. Herein I report on a natural hybrid between *B. cognatus* (Great Plains toad) and *B. punctatus* (red-spotted toad), members of separate species groups within the "thin-skulled" lineage of North American toads.

The hybrid male was collected in a rain-formed pool on the evening of 13 August 1990 at the Cave Buttes Recreation Area along Cave Creek, 12 km southwest of Cave Creek, Maricopa County, Arizona. Approximately 50 mm of rain fell from 11 to 13 August; on each evening, a number of anurans called along a narrow (3-m wide), flowing stream and a large, shallow pool (40-m diameter) created by an earthen dike across the stream channel. Male *B. alvarius*, *B. cognatus*, and *Scaphiopus couchii* called from the pool, while male *B. punctatus* were restricted to the channel.

The hybrid was calling among the male *B. cognatus* at the large pool. I recorded a series of its advertisement calls using a Marantz PMD 430 cassette recorder and Sennheiser ME-80 microphone, and I measured its cloacal temperature with a Weber Quick Recorder thermometer. Five calls were analyzed with a DATA Precision 6000 Waveform Analyzer (see Sullivan 1989 for details), and mean values were calculated for each call variable. Data are reported as the mean ± standard deviation.

The mean pulse rate of the advertisement call of the hybrid was 45 p/s, and the mean duration was 7.8 s, at a cloacal temperature of 24 C. The corresponding values for 13 *B. punctatus* recorded on the same night were 55 ± 2.60 p/s and 6.4 ± 1.23 s (cloacal temperatures = 25 ± .34 C); the values for 8 *B. cognatus* were 24 ± 1.66 p/s and 18 ± 7.58 s (cloacal temperatures = 25 ± .82 C). The dominant frequency of the hybrid's advertisement call was 2.109 kHz, lower than both *B. punctatus* (2.538 ± .111 kHz) and *B. cognatus* (2.700 ± .207 kHz). Hence, the advertisement call of the hybrid, although more similar to that of *B. punctatus*, was intermediate in pulse rate and duration and dramatically lower than either parental species in dominant frequency. However, the vocal sac was darkly pigmented and sausage-shaped when inflated (Fig. 1), the condition typical of *B. cognatus*.

The hybrid was intermediate in size (63 mm snout-vent length) relative to *B. punctatus* (54 ± 2.59 mm) and *B. cognatus* (75 ± 4.83 mm). The oval parotoid glands, enlarged cranial crests, and boss of the hybrid were also intermediate to *B. cognatus* and *B. punctatus*. Following the methodology of Ferguson and Lowe (1969), I determined four ratios (parotoid length/parotoid width, svl/parotoid width, parotoid length/eyelid length, tibia/parotoid length) for the two parental species and the hybrid. All of the ratios calculated for the hybrid were between the mean values and exclusive of the 95% confidence intervals for the two parental species.

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Unfortunately, the hybrid escaped after these observations were completed. Documentation of a natural hybrid between members of these two distinct species groups is noteworthy. Although *B. cognatus* and *B. punctatus* typically breed in dissimilar habitats, the present observations reveal that they may interact if they breed sympatrically, and that they can produce hybrid offspring. Additional work will be required to determine the evolutionary importance, if any, of such interactions.

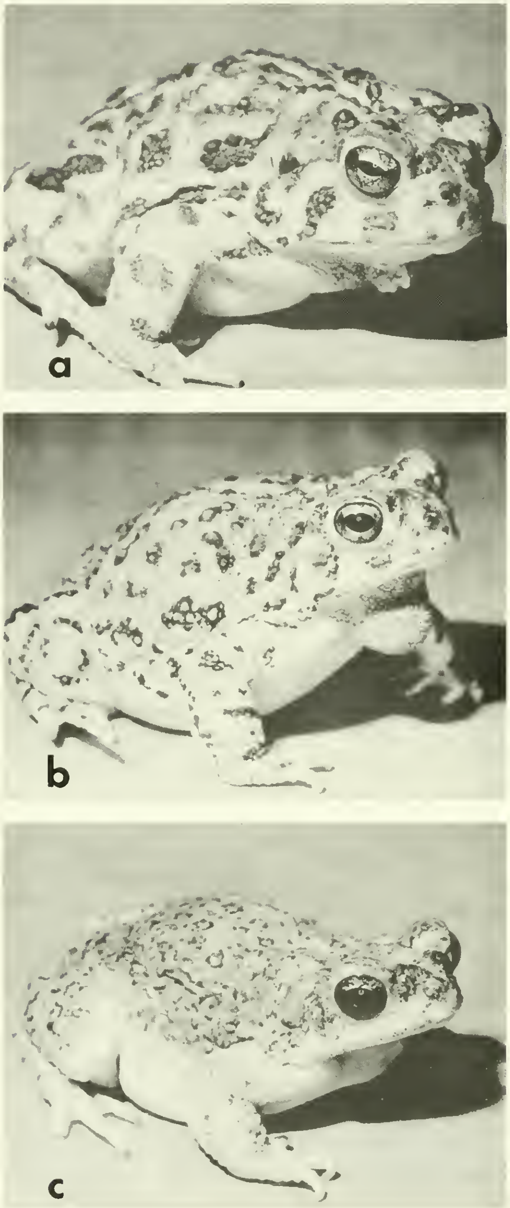

Fig. 1. (a) *Bufo cognatus*, (b) hybrid, and (c) *Bufo punctatus* from Cave Buttes Recreation Area, Maricopa, County, Arizona.

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NEW VARIETY OF *OXYTROPIS CAMPESTRIS* (FABACEAE) FROM THE COLUMBIA BASIN, WASHINGTON

Elaine Joyal[1]

In 1984 I found an *Oxytropis* in central Washington that I was unable to identify. Collection was made and sent for determination to Rupert Barneby, who puzzled over it for some time before concluding that it lacked a published name. What follows is a description of that taxon. This is a rare taxon, presently known from a single population on an isolated mountain. Habitat and ecological notes are included, therefore, to facilitate understanding of the taxon's conservation status.

Oxytropis campestris (L.) DC. var. *wanapum* Joyal, var. nov.
Fig. 1

O. campestri (L.) DC. var. *gracili* (A. Nels.) Barneby affinis, plantis dense sericeo pilosis, robustis, foliolis 20–25, corollis lavandulis, carinis maculatis, differt.

Caespitose perennial, acaulescent, 17–30 cm tall; herbage silvery, densely silky-pilose to villous; stipules membranous, pilose to densely pilose, the blades free for half their length, (5) 6.5–9 (16) mm long, margins ciliate to densely ciliate; leaves (11) 14–18 (22) cm long, with (13) 19–26 (32) linear to narrowly oblong leaflets, (8) 15–25 (33) mm long, scattered, sub-opposite; scapes erect to spreading, (10) 17–21 (30) dm long, pubescence spreading-appressed; racemes in part exceeding the leaves, (5) 6–12 (17) flowered, congested in flower, (4) 6–8 (12) cm long in fruit; calyx sericeous-pilose, 7–9 mm long, greater than half the length of the corolla, with a few dark hairs, the tube 5–7 mm long, the teeth (1) 2–3 mm long, linear-lanceolate; corolla pale lavender with darker penciling, keel maculate, drying blue; banner obovate, 14–16 (23) mm long; wings 13–15 (19) mm long; keel (10) 11–14 (17) mm long; pod sessile to short-stipitate, erect, 1-celled with the suture not or only slightly intruded, the wall membranous-leathery, 10–20 mm long, beak about 6 mm long.

TYPE: UNITED STATES: Washington, Grant County, Saddle Mountain, above Lower Crab Creek and E of Beverly, T15N, R24E, S2, N1/2, elev. ca 550 m, NNE aspect at crest of ridge, in sandy (volcanic ash) soils above steep basalt talus, 25 May 1987 (flower and early fruit), Joyal 1264 (Holotype: US; Isotypes: BRY, CAN, CAS, ISC, K, MO, MONTU, NY, OSC, S, UBC, WS, WTU).

PARATYPE: UNITED STATES: Washington, Grant County, Saddle Mountain, above Lower Crab Creek, T15N, R24E, S2, elev. ca 550 m, NNE aspect at crest of ridge, in sandy soil, 15 May 1984 (flower), Joyal 467 (BLM—Spokane, NY, OSC).

There are currently at least 10 varieties of *O. campestris* recognized in North America (Barneby 1952, Elisens and Packer 1980, Welsh, personal communication). Characters used to distinguish the infraspecific taxa are: length of leaves and of scapes, number of leaflets, numbers of flowers per raceme, length and density of flowers in raceme, color of corolla, habitat, and distribution. There are notable differences in these characters in variety *wanapum* when compared with other varieties of *O. campestris*. The three varieties that occur in eastern Washington with var. *wanapum* are compared below; a key also is provided to separate these four varieties (see Barneby 1952, Elisens and Packer 1980, Welsh, personal communication, for comparison with other *O. campestris* varieties). On the average, plants of var. *wanapum* are more robust and have a greater number of leaflets. The length of the leaves (16 cm) averages

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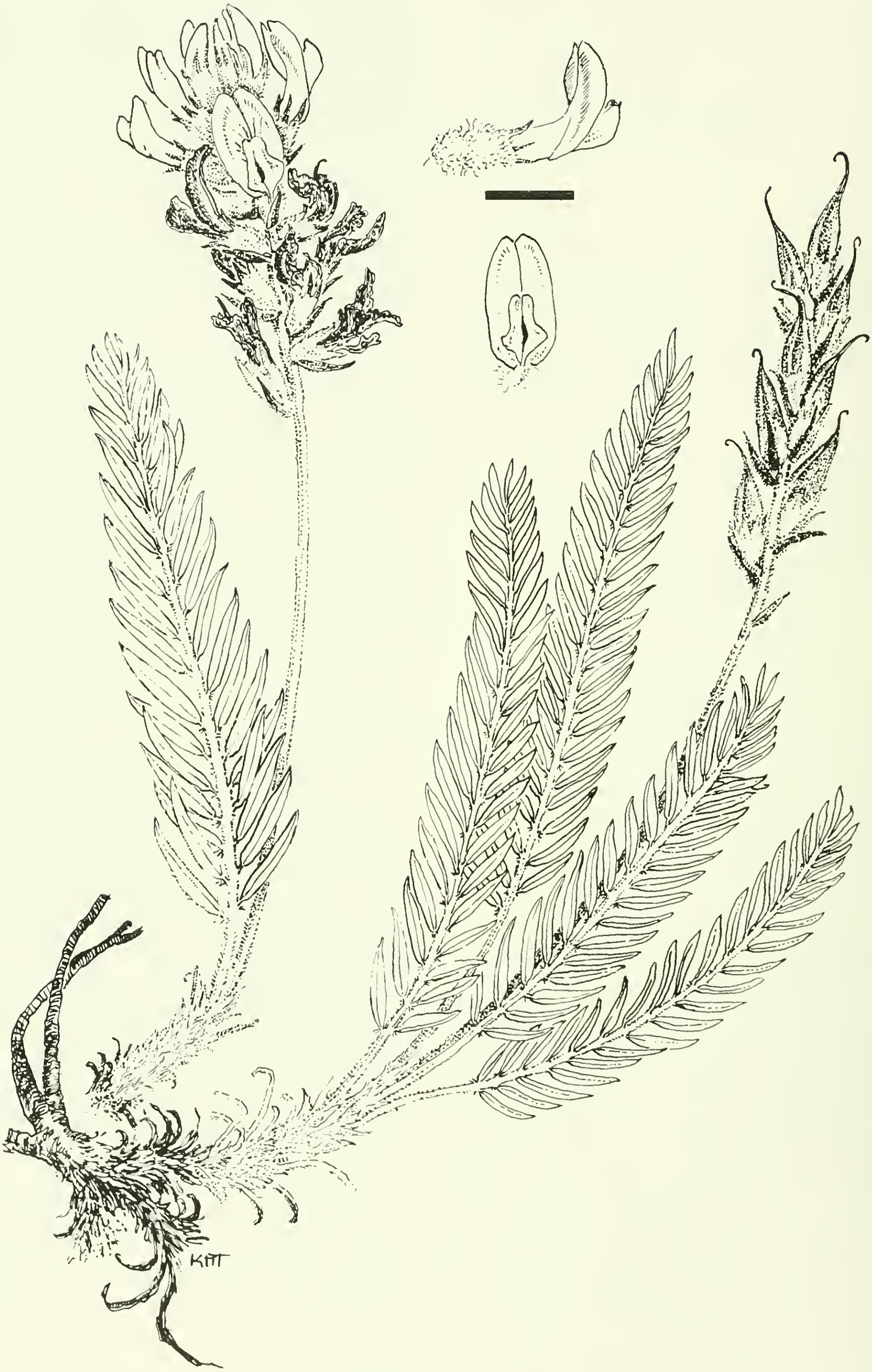

Fig. 1. *Oxytropis campestris* var. *wanapum*. Habit. Flower (bar = 1 cm). Composite drawing from Joyal 467, 1264, and photos of the Saddle Mountain population.

greater than those of var. *columbiana* (St. John) Barneby, *cusickii* (Greenm.) Barneby, and *gracilis* (A. Nels.) Barneby (11, 6, and 11 cm, respectively); leaflet length (20 mm) likewise averages greater than those of the other three varieties, (14, 8, and 12 mm); scape length (20 cm) is also greater than the other three (17, 7, and 16 cm); the mean number of leaflets (22) is greater than the first two varieties (each = 15) and within the range of the third variety (17); the average number of flowers per raceme (8.5) is within the range of three related taxa (8–12), with *columbiana* and *gracilis* occasionally having as many as 30 flowers/raceme; keel length (12 mm) is similar for all four taxa, with *gracilis* showing slightly larger dimensions; the pale lavender flower color, while not unique in the group, is unknown among northwest members of *O. campestris*. Some of these differences might be explained as a phenotypic response of a primarily montane taxon to a desert environment. Its desert habitat sets this taxon apart from its close relatives in nearby mountains; precipitation is about half that of the mountains (20 cm vs 40 cm/yr), the climate is warmer, the vegetation is shrub-steppe rather than forested, the geologic substrate is sedimentary and volcanic rather than intrusive with some volcanic rocks, and it lies south of the glaciated portions of the Okanogan Highlands and Cascade Range.

Key to closely related varieties of
Oxytropis campestris in the Pacific Northwest
(after Hitchcock and Cronquist 1973)

1 Corolla white with maculate keel; leaflets 12–17 (23); in wet gravel along the Columbia River in Washington (historically) and near Flathead Lake, Montana .... var. *columbiana*

1′ Corolla other than white with maculate keel; leaflets often more than 17

2 Stipules glabrous or glabrate; scapes rarely greater than 15 cm; leaflets seldom greater than 17; range of var. *gracilis*, but not above 2000 m elevation and not west of the Cascades .... var. *cusickii*

2′ Stipules very hairy; scapes mostly greater than 15 cm; leaflets generally greater than 17

3 Corolla ochraleucous or white, keel rarely maculate; leaflets 15–20; plants averaging smaller than the next, scapes averaging 16 cm; usually montane plants (in prairies east of the Rocky Mountains); western Washington to Alberta and South Dakota, south in Rocky Mountains to Colorado .... var. *gracilis*

3′ Corolla pale lavender with darker penciling, maculate keel, drying blue; leaflets 20–25; plants larger than the preceding, scapes averaging 20 cm; desert plants; at low elevation in the Columbia Basin of central Washington .... var. *wanapum*

Elisens and Packer (1980) most recently treated the *O. campestris* complex in northwestern North America. They introduced new cytological information for several of the taxa in this difficult complex; on the basis of these data they reelevated several taxa, including the eastern Washington var. *columbiana*, to full species status. While accepting their findings, I do not see that it necessarily follows that taxa such as *O. campestris* var. "*columbiana*" should be given specific status based on Elisens and Packer's new data. More importantly, Barneby (personal communication) and I agree that it is preferable to treat the undescribed taxon in a conservative fashion and place it at what we consider the appropriate rank as a variety of *O. campestris*, near var. *gracilis*. It may well be that future studies (Welsh, personal communication) in the *O. campestris* complex will result in this entity being raised to a higher rank. However, until that work is completed, varietal status under *O. campestris* seems more appropriate.

Oxytropis campestris var. *wanapum* is presently known only from Saddle Mountain in the Columbia Basin of central Washington (Fig. 2). Saddle Mountain is an isolated east-west trending ridge formed from a partly faulted anticline that stretches approximately 50 km, being cut by the Columbia River at Beverly. Several ranges to the southwest conceivably may contain habitat suitable for var. *wanapum*. Whereas the north slope is steep basalt talus, the south slope is gentle and sandy and dominated by *Artemisia tridentata*. The *Oxytropis* grows in a narrow band of deep sand, derived from volcanic ash, slightly below the crest of the north-facing ridge. The community is very open, as is typical of many sandy habitats. It is dominated by *Chrysothamnus nauseosus*, *Salvia dorrii*, *Monardella odoratissima*, *Agropyron spicatum*, and *Bromus tectorum*. Other species present include *Achillea millefolium*, *Arenaria franklinii*, *Astragalus caricinus*, *A. purshii*, *Castilleja* cf. *thompsonii*, *Chaenactis douglasii*, *Comandra umbellata*, *Crepis modocensis*, *Cryptantha pterocarya*, *Erigeron linearis*,

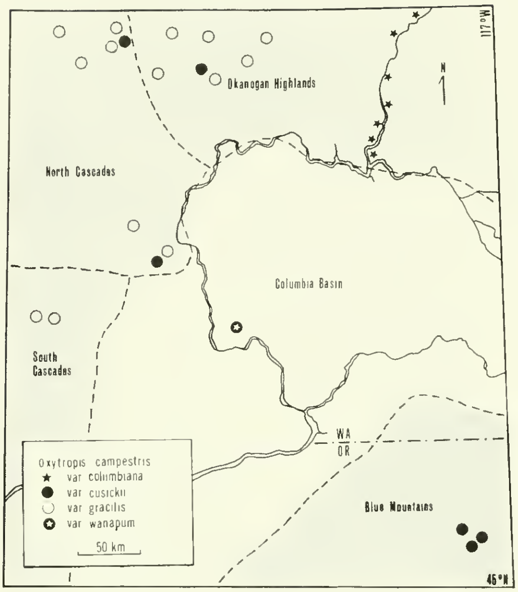

Fig. 2. Distribution of *Oxytropis campestris* varieties in eastern Washington and adjacent Oregon. Data points are of representative specimens from MO, OSC, US and WTU. Elevations in the Columbia Basin physiographic province average less than 500 m (unshaded); those in the Blue Mountain, North and South Cascade, and Okanogan Highland physiographic provinces average greater than 500 m (shaded).

Eriogonum microthecum, *E. ovalifolium*, *Eriophyllum lanatum*, *Galium multiflorum*, *Gilia sinuata*, *Hackelia arida*, *Lupinus* sp., *Penstemon richardsonii*, and *Poa* sp. (taxonomy follows Hitchcock and Cronquist 1973). No other *Oxytropis* spp. were noted in the immediate vicinity.

Plants of this taxon are frequent (several hundred individuals) in this restricted area, and there is a good size-class distribution of individuals. I observed seedlings, which I presumed to be from the previous year, small vegetative individuals, and flowering plants. The largest plants had many flowering stems (as many as 48 stems per plant observed) and covered areas up to 0.5 meter across. This *Oxytropis* flowers profusely. My first collection of the taxon was made at peak flowering, in the middle of May 1984, an average season with respect to temperature and precipitation. During my second visit in late May 1987, an early and dry spring, I found the plants mostly past flower and well into fruit. The flowers of this *Oxytropis* are held at a 45-degree angle from the rachis, or higher, becoming erect in fruit. The only floral visitors I observed were several iridescent blue-green metallic-leafcutter bees (*Osmia integra* Cresson, Hymenoptera: Megachilidae), working *Oxytropis* flowers on the upper slope. The pods have a short pubescence and redden as they mature. Seed set appeared to be good, but predation of seed pods was high. Some pods had their sides chewed out in a pattern typical of departing larvae with not a single seed remaining within; more often the upper one-half or one-third of the pod had been eaten away entirely, along with all developing seeds. No larvae were observed, but several small weevils collected from the pods were identified as species of *Tychius* (Coleoptera: Tychinae).

Oxytropis campestris var. *wanapum* occurs on land that is a "checkerboard" of Bureau of Land Management (BLM) and private lands. The primary land use is grazing; some recreational vehicle use occurs on the mountain as does natural gas exploration. The area in which the *Oxytropis* grows is isolated by low rimrock from the bulk of the grazing activity to the south. The BLM's Spokane District is treating the taxon as a "sensitive" species.

The varietal epithet honors the Wanapum tribe, who originally called Saddle Mountain and the desert surrounding it home. The Wanapum, except for one small community on the south side of the mountain, have mostly disappeared from the landscape.

ACKNOWLEDGMENTS

The original discovery of this taxon was made while I was employed by the Spokane District Office of the Bureau of Land Management, U.S. Department of Interior. Gary Parsons identified insects; Richard Rust provided the specific epithet for *Osmia;* Kay Thorne did the illustration; Kenton Chambers of Oregon State University provided work space and herbarium support on a regular basis during my western tenure; the Smithsonian Institution staff has generously allowed me use of their herbarium; and Rupert Barneby and Stan Welsh provided valuable comments on the manuscript. I am especially indebted to Rupert Barneby, for whom I first thought of collecting this taxon. It was he who later confirmed why I was unable to put a name on it, and who encouraged me to write this paper.

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EFFECT OF BACKPACK RADIO TRANSMITTER ATTACHMENT ON CHUKAR MATING

Bartel T. Slaugh[1,3], Jerran T. Flinders[1], Jay A. Roberson[2], and N. Paul Johnston[3]

Results of a previous study (Slaugh et al. 1989) indicate that backpack radio transmitter attachment is more compatible with Chukars (*Alectoris chukar*) than is a poncho apparatus. It appears, though, that backpacks, especially the antenna angle, could inhibit Chukar mating. The objective of this study was to determine the effects, if any, of backpacks and antenna position on mating and fertility.

Materials and Methods

Chukars were housed (as pairs or trios) in 45-cm-high × 75-cm-wide × 90-cm-long wire cages. Six pairs had no radio transmitters attached (group I). In group II each of six cages contained one male and one female without radios plus one female with a simulated backpack radio with the antenna angled downward along the tail (Fig. 1). In group III each of six cages contained one male and one female without radios plus one female with a simulated backpack radio with the antenna angled upward (Fig. 1). The purpose was to determine if the males would prefer to mate with the females without radios and exclude the females with radios. Eggs were collected from females for one week prior to exposure to males to ascertain fertility status. Females were exposed to males for four days and then separated and caged individually to facilitate individual fertility observations. Eggs were collected for one week, incubated for one week, and then opened to determine fertility.

Results and Discussion

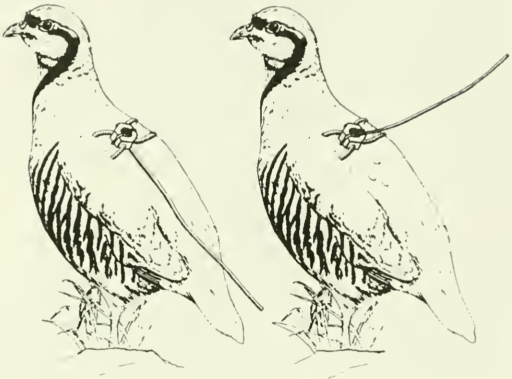

Fig. 1. Backpack attachment of simulated radio transmitters with antenna angled downward (left) and upward (right).

Females in all groups produced fertile eggs, indicating that males did not exclude radio-attached females from their mating. The radios and antennae did not impair mating even when antennae were angled upward. Males were observed to either straddle the antenna or grasp it with a foot and bend it downward while mating. These results indicate no mating problems with captive Chukars fitted with radio transmitters. Their behavior, however, could possibly differ in the wild.

This study did not include any field observations of mating or fertility. The only problem observed with released Chukars carrying backpacks was that, with the antenna angled upward, some birds experienced difficulty in flying as a result of a wing coming in contact with the antenna. Attachment one week prior to release (to allow time to become accustomed to radios) did not affect flight ability or survival.

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FOOD CACHING AND HANDLING BY MARTEN

Stephen E. Henry[1], Martin G. Raphael[2], and Leonard F. Ruggiero[1]

Various studies provide evidence of food caching by marten (*Martes americana*). Marten have been seen uncovering or retrieving food items (Murie 1961, Simon 1980, Buskirk 1983), but whether these items were initially cached by marten was unknown. Hawbecker (1945) and Thompson (1986) documented food concealment by marten, but neither reported subsequent recovery of prey. Due to lack of evidence, Stordeur (1986) concluded that caching of food is uncommon in marten. Prey caching has important implications for foraging frequency and energetics of marten.

Study Area and Methods

The primary objective of our research was to quantify changes in marten home range characteristics and habitat use following the fragmentation of a subalpine coniferous forest. An ancillary research objective was to describe the characteristics of marten resting sites. Our study area was in the Medicine Bow National Forest, 18 km south of Encampment, Wyoming. The area was characterized by stands of lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*). Small meadows and rock outcrops were interspersed throughout the area. Elevations at the observation sites ranged from 2935 to 3387 m.

Most observations were made during field efforts to locate resting sites of radio-collared marten. Resting sites were defined as locations in which a marten remained stationary and inactive for at least 0.5 h. The radio-signal strength was monitored for 0.4–1.5 h from a distance of at least 70 m. After the signal indicated inactivity, the potential resting site was quietly approached on foot to avoid alerting the marten or causing it to flee. Precautions were made to minimize the observer's influence in order to maximize observations of natural behavior. These precautions included reduction of receiver volume, concealment of the observer, and removal of shoes if necessary.

Observations

Case 1.—9 June 1987, 1445 h. Adult male marten M3 was seen carrying the hind half of a snowshoe hare (*Lepus americanus*) for about 20 m near a known resting site. He cached the hare under a leaning stump and then foraged within 400 m for about 0.5 h before returning to the hare and carrying it away.

Case 2.—8 July 1987, 1015 h. M3 was seen foraging in and around a rock outcrop. After 5 min the marten emerged from the rocks, grasping a juvenile yellow-bellied marmot (*Marmota flaviventris*) by the neck. He immediately carried the prey approximately 550 m, deposited it in a rock crevice in a road fill, and then left the site. There were six marten scats at the entrance of this den, indicating prior use by this or other marten.

Case 3.—1 September 1987, 1900 h. M3 was found resting in a bushy-tailed wood rat (*Neotoma cinerea*) nest in a rock outcrop. He growled a few times and then ran away, carrying an unidentified mammal.

Case 4.—9 September 1987, 1730 h. M24 was found resting in a rock outcrop. As the observer approached, the marten peered from a crevice before disappearing back into the rocks. After a few seconds he emerged and fled, carrying a chipmunk (*Tamias* spp.).

Case 5.—22 September 1987, 1300 h. M3 was seen feeding on a freshly killed Blue Grouse (*Dendragapus obscurus*) next to a large log. The marten carried the grouse about 40 m and cached it in branches of a recently felled pine, then retreated to a nearby resting site under a different log. Two Blue Grouse feathers, one Northern Flicker (*Colaptes auratus*) feather, and two Gray Jay (*Perisoreus canadensis*) feathers were found at the entrance to the resting site. After 25 min the marten ran from the den, took the grouse, and headed downslope.

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CASE 6.—27 July 1988, 1605 h. The observer heard F28 killing a juvenile Blue Grouse in an alder (*Alnus tenuifolia*) bog. A few minutes later she was observed eating the grouse inside a hollow log approximately 25 m from the kill site. During this time an adult grouse was heard giving the brood-gathering call. When one of the young responded with a call, the marten left the dead grouse in the log and stalked the live young. It located a young grouse in a tree and made an unsuccessful attempt to catch it. Upon returning to the original prey, the marten saw the observer and left without the cached grouse. The prey had been removed from the log by 1400 h the following day.

CASE 7.—31 January 1989, 1240 h. M35 found a piece of beaver meat (trap bait) at our field camp. He carried the meat 15 m away, climbed up a tree, and moved out onto a limb heavily laden with snow. He dug a hole in the snow, placed the meat in it, and then covered the meat with snow before descending the tree. He continued to move about the camp area, searching for additional food.

CASE 8.—26 July 1989, 0710 h. A hidden observer witnessed M35 cache a red squirrel (*Tamiasciurus hudsonicus*) under a shelter at the field camp. After caching, the marten immediately left. Approximately 12 h later (1930 h), M35 was observed retrieving the squirrel.

CASE 9.—3 August 1989, 1050 h. Red squirrels were heard scolding F37 at their midden. At 1115 h the marten was seen at the base of a snag 150 m from the midden. She had a squirrel forearm in her mouth as she ascended into the broken top of the snag. Within moments she descended without the forearm and left the area. Inside the snag was found the squirrel forearm and the hind one-third of a squirrel. Within an hour the marten was out of telemetry range.

DISCUSSION

For our purposes "caching" is defined as the act of concealing food for later consumption. Marten meet the criteria for "cachers" (Macdonald 1976); viz., they are solitary hunters with fixed home ranges, and they are not large enough to protect their prey from larger scavengers. Our observations show that marten will cache large prey items, and cases 1, 5, and 8 are rare documentation that the same individual that made the cache had subsequently returned to it. In addition, these observations show that sometimes the cache site also serves as a resting site or den. We have also documented hunting behavior that is generally associated with surplus killing.

Small rodents are consumed quickly by marten, and they are not necessarily removed from the kill site (Pulliainen 1981b). However, it has been reported that marten readily carry larger prey from 9 m to several hundreds of meters away from kill sites (Murie 1961, Hargis 1981, Pulliainen 1981b, Raine 1981, Spencer and Zielinski 1983). Our observations (cases 1, 2, 5, 7, 8, 9) demonstrate that marten cache food at varying distances from kill sites, especially if the prey is too large for one meal. We suggest that the removal of prey from capture sites may provide security for marten. The noise of the pursuit and kill (e.g., cases 6 and 9) and the distress calls of the prey could alert competitors or predators to the location of a marten and its kill. This is consistent with observations made by Simon (1980), who found that marten typically consume food in secluded cover.

Cases 2, 3, and 4 are similar to the findings of Pulliainen (1981a), Raine (1981), and Spencer (1981), who also observed that marten sometimes carry prey items to their resting sites. The selection of a resting site may depend upon the proximity to the kill site (Marshall 1951, Buskirk 1984) and the amount of protection afforded. When a marten uses a specific rest site on consecutive days (e.g., Steventon 1979), it may be because of cached food.

In Finland, Pulliainen (1981b) found surplus killing of prey by European pine marten (*M. martes*). Our observations (cases 1, 6, 7, 8, 9) suggest that marten participate in surplus killing. Animals that we observed resumed an apparent foraging activity after caching.

Marten meet the criteria for species prone toward surplus killing, suggested by Oksanen et al. (1985), because they are small members of a predator guild in a cool, dry environment (at least throughout portions of their range). However, there is no evidence suggesting that marten are involved in surplus killing or hoarding to the same extent as other mustelids (e.g., Johnsen 1969 [as cited in Oksanen 1983] reported a stoat's [*Mustela erminea*] single cache of 153 lemmings and a shrew). Important knowledge of marten ecology would be gained if researchers could devise a way to examine the interior of resting sites to determine if food caches vary seasonally.

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HOLOCENE PREDATION OF THE UINTA GROUND SQUIRREL BY A BADGER

Michael E. Nelson[1]

In 1985 J. H. Madsen, Jr., then the state paleontologist of Utah, collected several fossil bones at an elevation of 1524 m in Morgan County, Utah (Utah Antiquities locality 42Mo029v). The specimens were recovered from a large burrow intruded into shoreline sands deposited by Pleistocene Lake Bonneville. All fossils were found in a single pocket that probably represents the distal end of a burrow of the North American badger, *Taxidea taxus*. The specimens consist of (1) numerous post-cranial elements of a juvenile badger and (2) several bones, including a right dentary, of the Uinta ground squirrel, *Spermophilus armatus*. Many of the ground squirrel bones are crushed or broken, a condition also noted by Long and Killingley (1983) in their study of badger prey.

Taxidea taxus is virtually an exclusive carnivore and does not eat significant amounts of plant material (Ewer 1973). Rodents are the most common prey, but the animals are not adverse to eating a variety of other vertebrates and arthropods (Long and Killingley 1983). Messick and Hornocker (1981) noted that Townsend ground squirrels, *Spermophilus townsendi*, are the most important prey species of badgers in southwestern Idaho. The animals either burrow after the active squirrels, catch them hibernating in their burrows, or opportunistically wait at a burrow entrance (Balph 1961). Badgers also will eat carrion and sometimes make food caches (Snead and Hendrickson 1942).

Postdeath disturbance of the bones probably accounts for missing elements of both *Taxidea* and *Spermophilus*. All preserved bones show extensive gnawing by small rodents; mice and other rodents commonly occupy badger burrows after the structures are deserted (Choate 1989, personal communication).

Part of the badger pelvis was sacrificed for a radiocarbon date completed by Tandem Accelerator Mass Spectrometry at the Laboratory of Isotope Geochemistry, University of Arizona. The date of 2790 ± 74 yr. B.P. (AA–2514) suggests that Holocene diets of Utah badgers were similar to their extant counterparts. The remains of the ground squirrel may represent the last meal of the badger.

All specimens are accessioned into the Sternberg Memorial Museum at Fort Hays State University (FHSM VP-10648 [ground squirrel] and FHSM VP-10649 [badger]). I thank Dr. Dave Gillette (Utah Antiquities), James H. Madsen (DINOLAB), and John Lund (FHSU).

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PATTERNS OF MICROHABITAT USE BY *SOREX MONTICOLUS* IN SUMMER

Mark C. Belk[1,2], Clyde L. Pritchett[1], and H. Duane Smith[1]

Sorex monticolus is found from Alaska to Mexico in a variety of montane and boreal habitats (Hennings and Hoffmann 1977). In previous characterizations of microhabitat used by this species, few measures of physical or vegetative structure were significantly correlated with captures of *S. monticolus*. Typically, only some measure of near-ground cover (or related variables) is significantly associated with abundance. *Sorex monticolus* favors habitats with dense ground cover but seems to have few other microhabitat requirements (Hawes 1977, Terry 1981, Gunther et al. 1983, Reichel 1986, Doyle 1989).

In most montane areas the annual cycle of snow accumulation and melting, followed by herbaceous growth and decay, causes large-scale changes in the near-ground environment. During summer rapid herbaceous growth greatly increases the area covered by dense, near-ground vegetation. Previous studies of microhabitat use by *S. monticolus* have not addressed temporal changes in habitat use relative to this change in available cover (Terry 1981, Doyle 1989).

During summer 1986, in conjunction with a study of microhabitat use by rodents in a montane area, we recorded 104 captures of shrews in Sherman live traps. These shrews all appeared similar, and 17 specimens, retained for positive identification, subsequently were identified as *S. monticolus*. Given the possibility that some of the shrews captured may have been another species, we used a binomial probability to calculate the proportion of the 104 captures that could be regarded as *S. monticolus;* at a .05 level of confidence at least 85% of shrews captured were *S. monticolus*. Based on this, we feel confident that the majority, if not all, of the shrews captured were *S. monticolus*. In this paper we examine temporal patterns of microhabitat use by these shrews during summer in relation to changes in microhabitat.

STUDY AREA AND METHODS

The study site (111°37′N, 40°26′W) is on the east slope of Mount Timpanogos at an elevation of about 2400 m in Utah County, Utah. The habitat includes stands of aspen (*Populus tremuloides*) and Douglas fir (*Pseudotsuga menziesii*) interspersed with herbaceous meadows and shrub-dominated ridges (principally snowberry, *Symphoricarpos albus*). Three trap grids were located in separate areas considered similar in overall habitat structure. Each grid covered 1 ha and contained 100 trap stations arranged in 10 rows of 10 each. Two folding Sherman traps were placed at each station, and stations were 10 m apart. Grids were trapped in a rotating fashion (see Belk et al. 1988 for details). Trapping began in early June, immediately after snowmelt, and continued until mid-September, resulting in 13,800 trap nights.

Nineteen habitat variables were measured at each trap site characterizing live woody structure (trees and shrubs), dead woody structure (fallen logs), and herbaceous cover and height (see Belk et al. 1988 for details). Five variables were correlated with shrew captures at the .10 level of significance during at least one month. These variables—percent canopy cover, average overstory tree size, average understory tree size, density of fallen logs, and number of woody species—were analyzed with principal-components analysis (SAS Institute, Inc. 1985). Two components had eigenvalues greater than one, but shrews exhibited little variation of habitat use on the second component (all means near

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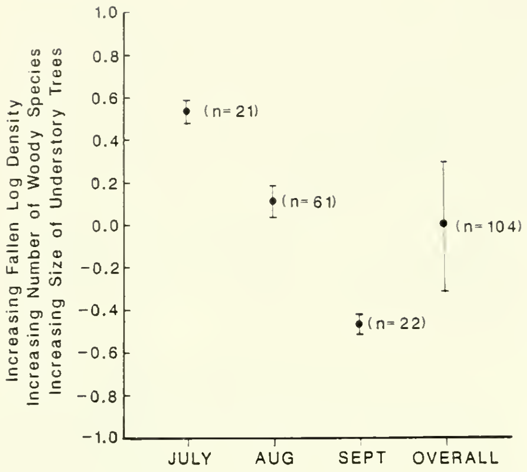

Fig. 1. Distribution of means and 95% confidence intervals of habitat use by shrews on the first principal component for July, August, September, and the entire summer combined.

zero). Accordingly, habitat use by shrews was interpreted only on the first principal component. This component (variable loadings in parentheses) described a gradient of increasing density of fallen logs (0.596), increasing number of woody species (0.628), and increasing size of understory trees (0.415).

RESULTS

No shrews were captured in June; 21, 61, and 22 captures of shrews were recorded for July, August, and September, respectively. Mean habitat use for the entire summer plotted on the first component appeared no different from a random sample (Fig. 1). However, investigation of habitat use partitioned by months revealed temporal variation in habitat use (Fig. 1). Thus, the pattern of habitat use generated from the entire sample was an artifact caused by averaging over time. Habitat used by shrews for each month was much less variable (variance ranged from 0.03 to 0.07) than simulated random samples, with sample sizes about equal to those observed for shrews (variance ranged from 1.28 to 1.81 for five simulations). Thus, it appears that shrews were using the habitat nonrandomly, and observed patterns of variation were not merely artifacts of limited samples.

Habitat use in July was characterized by areas with higher densities of fallen logs, greater numbers of woody species, and larger size of understory trees. This was characteristic of shrubby areas in earlier stages of succession. In August mean habitat use was close to the overall mean of available habitat, representing areas with intermediate values of habitat variables. In September shrews used habitat with lower densities of fallen logs, fewer numbers of woody species, and smaller understory trees, representing areas dominated by climax aspen stands (Fig. 1).

DISCUSSION

No variable or combination of variables was characteristic of habitat used by shrews across all months. Rather, since characteristics of woody vegetation changed little during the summer, it appears shrews are responding to temporal change in the near-ground environment caused by rapid herbaceous growth during early to mid-summer (occurring first in open areas), followed by dessication and matting down of herbaceous growth as autumn approaches. In early summer, soon after snowmelt, areas lacking woody vegetation were mostly bare, having only a thin, compacted layer of litter. Correspondingly, habitat used by shrews included woody ground cover such as fallen logs and shrubs. At the height of the summer season, a few weeks later, herbaceous growth 0.5–1.5 m high covered the entire study area, and most of the habitat was probably suitable for use by shrews. By September herbaceous growth persisted in mesic sites under dense canopies provided by aspen stands, but herbaceous cover in open areas was declining. Accordingly, habitat used by shrews shifted toward areas dominated by mature aspen stands. Such tracking of ground cover by *S. monticolus* accords with previous descriptions of microhabitat use by this species (Terry 1981, Doyle 1989).

Comparison of patterns of microhabitat use between shrews and four species of rodents (*Peromyscus maniculatus*, *Zapus princeps*, *Clethrionomys gapperi*, and *Microtus montanus*) in the same area reveals a strong contrast. Rodent abundance was strongly correlated with 13 habitat variables, and rodents showed strong patterns of habitat partitioning based on these variables (Belk et al. 1988).

Shrew captures were weakly correlated with only five variables and showed relatively little variation on these variables. In this study area coexistence of several rodents may necessitate habitat partitioning, whereas S. *monticolus* appears to be the only shrew in the area (at least other species are rare). However, even when other species of shrews are present, S. *monticolus* is only weakly associated with measurements of physical or vegetative structure (Terry 1981, Doyle 1989). In conclusion, use of microhabitat by S. *monticolus* is strongly affected by temporal variation in distribution of ground cover, and this should be taken into account in future studies of microhabitat use and partitioning by shrews.

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THE

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